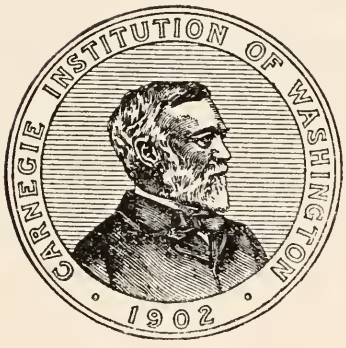
SIZE INHERITANCE IN RABBITS

By E. C. MACDOWELL

WITH A PREFATORY NOTE AND APPENDIX

By W. E. CASTLE



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PREFATORY NOTE.

In 1909 my pupils and I described certain preliminary studies of size characters in successive generations of rabbits bred chiefly for a study of color inheritance. We reached the provisional conclusion that total body-weight and skeletal dimensions are subject to *intermediate* or *blending* inheritance and do not conform with Mendel's law, as this law was then understood and as it was understood by Mendel himself. This conclusion seems to me still sound. But almost immediately after the publication of our paper the whole matter of blending inheritance was placed in a new light by the work of Nilsson-Ehle (which then came to my notice for the first time). Accordingly my experiments with rabbits were straightway arranged to show if possible whether or not blending inheritance is (as suggested by Nilsson-Ehle) really Mendelian, but without the occurrence of dominance and with several independent factors concerned in producing the observed results. These experiments were intrusted to Mr. MacDowell in the fall of 1909 and by him continued under my supervision until June 1912, when the results which he had obtained were presented in the form of a dissertation for the degree of doctor of science.

A number of animals not then mature have since furnished material which is incorporated in this publication.

While these studies were in progress several different investigations of size-inheritance in plants were published which have favored the interpretation of Nilsson-Ehle (and also of my colleague, Professor East) that in all inheritance, whether blending or not, Mendelian factors are concerned. Very naturally Mr. MacDowell has been strongly influenced by this idea, which seems to unify, if not to simplify, our conceptions of the method of inheritance. While not entirely sharing his views, I have tried not to bias his judgment either for or against the multiple-factor hypothesis which he adopts in this paper. But to avoid misunderstanding, I wish to say that in my own opinion the theory of the purity of the gametes has not been established, and too great definiteness and fixity is ascribed to Mendelian units and factors in current descriptions of heredity; consequently, too great importance is attached to hybridization and too little to selection, in explaining evolution.

But neither my views nor Dr. MacDowell's should bias the judgment of the reader. We wish to place before him clearly the results of experiments which have entailed much painstaking observation; the correct interpretation will become evident in due time.

These experiments have been made possible by a grant from the Carnegie Institution of Washington, for which grateful acknowledg-

ment is here made. I should not fail to mention also the indispensable facilities and helps of various sorts provided through the unfailing interest and kindness of Dean W. C. Sabine, of the Graduate Schools of Applied Science of Harvard University. Thanks are also due to my assistants, Messrs. S. Wright and H. D. Fish, who have helped with statistical computations as indicated in the text.

W. E. Castle.

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E. C. MACDOWELL

PART I.—HISTORICAL.

THEORY OF MULTIPLE FACTORS.

So much hybridization capable of a Mendelian interpretation has been performed in the last ten years that there remains little doubt, in the minds of investigators, that Mendel's Law is a correct description of the inheritance of certain types of characters. Of the three striking parts of this law, dominance, second generation ratios, and segregation, the last has come to be used almost synonymously with Mendelism. Cases showing the lack or imperfection of dominance are very common; a hybrid may even appear with a character entirely different from any possessed by either parent; the simple Mendelian ratio $([1+2]+1)^n$ has been found to be variously modified; but the seeming individuality, the apparently non-mixing nature of the substances upon which visible characters depend, stands firmly as the basis of Mendelism. So, when segregation is found, it may be said that the characters which show it are inherited in a Mendelian fashion. Segregation need not mean the reappearance of the parental combinations of characters in the second filial generation. Its primary theoretical conception is that the units that entered the first hybrid generation are uncontaminated in its germ cells, and as these units are independent every combination of them may appear in the next generation. An indication of segregation is the appearance in the second generation of forms never found in the first generation. If the parents differed by many characters it would be very unlikely that, in a small second generation (F_2), any form genetically like either parent would result from recombination, yet perfect segregation might occur.

It would be possible to produce and cross two strains of garden peas one of which was homozygous for all the seven dominant characters that Mendel investigated, while the other was homozygous for the seven corresponding recessive characters—that is, lacking all the dominant characters. Such plants would be characterized as follows: (1) Seed, smooth (A), yellow (B), with gray seed coat (C); pods, green (D), inflated when dried (E); habit, tall (F); flowers, axial (G). (2) Seed, wrinkled (*a*), green (*b*), with white seed coats (*c*); pod, white (*d*), when dried leathery (*e*); habit, dwarf (*f*), flowers, terminal (faciated) (*g*). The gametic formulæ would be ABCDEFG, and *abcdefg*. The first-generation hybrids would have the appearance of the dominant parent; their zygotic formula would be A*a*B*b*C*c*D*d*E*e*F*f*G*g*. Since each of these seven pairs of units is separate and independent, every possible combination of them will be found in the germ cells of this first generation, namely 128 (following Mendel's formula 2^n, where n equals the number

of character differences). Since any pair of these combinations may meet in forming an individual of the next generation there will be 2,187 possible zygotic combinations. (Mendel's formula $=3^n$). Lang (1910), using a method first introduced by Punnett, gives a table of the zygotic combinations in F_2 of a cross involving three character-differences. In the present case each dominant character is found to give in F_2 a simple 3:1 ratio to its absence. The formulæ of their frequencies one by one would be, $AA+2Aa+aa$; $BB+2Bb+bb$; $CC+2Cc+cc$, etc. The combined product of all these frequencies will give the frequencies of all the combinations found in the second generation. Their sum is 16,384 (Mendel's formula $= 4^n$). It is readily seen that there will be only one term that lacks all the large letters, as did the "recessive" parent. This is the product of the last terms of the individual frequencies. In every 16,384 F_2 individuals there will, in the long run, be only one plant looking like the recessive parent. There will be many apparently like the dominant parent, but individuals with identical breeding possibilities will occur no more frequently than forms resembling the recessive parent. The product of the first terms of the individual frequencies is the only homozygous dominant combination possible. The great number of individuals will have about half the dominant characters and half the recessive characters. Although over 16,000 plants would be required to find the parental combinations, 100 would clearly show segregation through the appearance of new associations of characters.

In the case of these seven characters of peas, dominance is practically complete. If a unit is present once—that is, if a character has come from only one parent—it is visible. But suppose there is no dominance and that a character received from one parent is only half as strong as when it is received from both. Smooth seeds by wrinkled would give slightly wrinkled seed; yellow by green seed would give pale yellow-green, etc. Thus since one "dose" could be distinguished from a double "dose," every zygotic combination would produce a different visible condition and the number of classes distinguishable would be 2,187.

Besides lacking dominance, imagine that these seven units all influence one character of one part. Let us assume, then, that the seed is given its characteristic yellow color by seven independent units or factors, each of which produces a shade of yellow. The presence of six of these units would produce a paler yellow and five a yellow paler still. And since dominance is lacking, intergrades would be formed due to the different effects of single and double "doses." In crossing a yellow with a green seeded plant, one that lacked all the units for forming yellow, the hybrid seed would have a uniform pale yellow color. Each unit would be present once, so that half as many units as in the yellow parent would be forming yellow, and the color produced would be half as strong. The same number of combinations would be found in the second generation as in the first case of the pea cross, but as each

unit by hypothesis is as strong as the next there would only be fifteen visible combinations—that is, fourteen grades of yellow forming a continuous series from strong yellow to solid green. As before, the pure yellow and green types would be found but once in 16,384 individuals. The most completely heterozygous combinations, as in the first case, would be most numerous, but the number in this class would be much greater, for here would fall all individuals that had combinations with seven of the possible fourteen "doses" present. In either direction from this group the frequencies would become smaller as they approached the extremes. They would form a curve very like the normal curve of error. Tammes (1911) gives a table of the distributions of the frequencies on similar assumptions with from one to six equivalent units involved. Castle (1911) represents the same thing graphically for two, three, and four characters.

EXAMPLES OF MULTIPLE FACTORS.

COLOR DIFFERENCES.

Such multiple factors as above described are not known to occur in pea colors, but comparable cases which may be explained by two or more independent factors giving rise to the same visible feature have been found by several investigators to whose work brief references will now be made. The important and conclusive investigations of Nilsson-Ehle gave rise to this theory of multiple factors. When oats with black glumes were crossed with varieties with white glumes, Nilsson-Ehle (1909) found that, in most cases, black behaved as a single unit-factor. In the second generation the ratio 3 black to 1 white was found. One variety of black oats, however, gave 630 black to 40 whites (15.8:1) in the second generation of a cross with white. This is a close approximation to the dihybrid ratio. Of the 43 F_2 plants carried to the third generation, 4 were white and showed no segregation, 17 were black and remained black in the next generation, while 22 were blacks which segregated into black and white. Of these, 11 gave 428 black and 120 white (=3.6:1); 9 gave 556 black and 35 whites (=15.9:1). Two of the F_2 blacks gave higher ratios which could be considered wide deviates from 15:1. Assuming, from the appearance of a dihybrid ratio in F_2, that two factors can produce black, it would be expected that in F_3 the whites would breed true, that in every 15 blacks 7 would remain black and 8 would segregate, 4 giving monohybrid ratios (3:1) and 4 giving dihybrid ratios (15:1). The results gave 17:11:9 (or :11, if the two families with higher ratios are included) =7:4.5:3.7 (or:4.5), whereas 7:4:4 was expected.

Among eight brown varieties of wheat, he found seven that gave monohybrid ratios when crossed with white, and one that gave a dihy-

brid ratio. The second generation consisted of 1,410 brown and 941 white (=15.0:1). Most red-grained wheats when crossed with white gave monohybrid ratios. Three strains, however, gave dihybrid ratios, while two were found that gave trihybrid ratios.

From these facts the general conclusion was drawn that quantitative differences in color can be brought about by the interaction of two or more independent factors, qualitatively similar, which segregate. These cases, although involving fewer character differences than were assumed in the hypothetical case of peas, show a very essential agreement with it. The number of different heritable grades of color in oats and wheat are much fewer than the supposed heritable grades of yellow in peas.

East (1910 and 1911) first presented evidence of the existence of two independent factors for the formation of yellow endosperm in maize. Although most lines with yellow endosperm gave monohybrid ratios when crossed with white, several gave very clear dihybrid ratios. The third and fourth generations showed close agreements with expectancies. Among pericarp colors East and Hayes (1911) have found five different reds. Two of these look fairly similar, but when crossed give whites in the second generation, in the proportions of 131 red to 7 white and 52 red to 2 whites. Tammes (1911) describes crosses between strains of *Linum* with different flower colors. A dark-blue and a light-blue strain when crossed with white gave simple monohybrid ratios in F_2. F_1 was intermediate. In the case of the light blue, the intermediate blue and parental type could not be easily separated, but the intermediates were in greater numbers. Crosses between two sorts of blue gave a second generation with a wide range of variability, the intermediate shades having the greatest frequencies. It was assumed that the blues used differed from each other in three units. It is possible that the monohybrid ratios—where (by comparison with Nilsson-Ehle's work) one would expect one dihybrid, if not a trihybrid ratio—do not depend upon the presence or absence of blue but upon the presence and absence of a color factor, as is the case of whites in other flowers and in animals.

The behavior of the various degrees of pigmentation of human skin, from black negroid to fair types, affords a suggestive comparison with the various shades of colors discussed in the preceding cases. Davenport and Davenport (1910) and Davenport (1911) and (1913) have presented evidence that supports the conclusion that the color of skin is due to various factors to whose cumulative effect the successively darker grades are due. In crosses between races with different grades of color these units segregate in the germ cells, but on account of their number the segregation is often seemingly imperfect and the parental characters are only more or less perfectly restored. Mudge (1909) gives a case of such segregation in which a "white" appeared in a quadroon family.

FORM DIFFERENCES.

From quantitative differences in color one is led to quantitative differences in shapes and forms. In crossing round and long varieties of *Brassica* roots Kajanus (1912) found an intermediate F_1 and an F_2 in which occurred distinct longs, various intermediates, and rounds in the proportions 1:14:1. To explain this and similar phenomena Kajanus assumes that there are two factors that lengthen the root (p. 225):

"Die jedes für sich bei doppelten Vorhandensein, und vereint bei einfachen Vorkommen eine zwischen ausgeprägt langer und ausgeprägt kurzer Form genaue Mittelstellung bedingen und bei sonstigen Kombination andere Formen zwischen lang und kurz hervorrufen."

Kajanus (1911) describes more complicated conditions in crosses with *Beta*. Nine types, fairly clearly separable, were recognized, ranging from flattened round to very long and slender. Thirty-two crosses were made and large numbers were obtained in F_2. The results show a fair degree of similarity with the following working hypothesis: There are two factors that influence length and two that influence roundness. Different combinations of these four factors and their absences account for the different types.

Emerson (1910) reports crosses between varieties of summer squashes and of gourds (*Cucurbita pepo*) which differ in shape of fruit. By a comparison of the coefficients of variability of F_1 and F_2, it was found that there was a marked increase in variability in the second generation.

This increase in variability is strikingly similar to the new grades of yellow in the theoretical case of yellow peas, to the grades of color in cereal crosses, and to the variety of forms found in the second generations of crosses of *Brassica* and *Beta*. Although Emerson makes no attempt to analyze the various grades in his crosses and no guess as to the number of factors involved, there seems little doubt but that (as he concludes) evidences of segregation are clear.

These two cases of shape differences involved incomplete dominance, or its absence. Shull (1911*b*) described a case in *Bursa bursa-pastoris*, in which two distinct form types are supposed to differ by two independent genes. The seed capsule in *Bursa bursa-pastoris* is flat and triangular; that of a recent mutant, *heegeri*, is oval; while in section it is round. The *pastoris* form is dominant; the *heegeri* form appears only in the absence of both the factors assumed to cause the *pastoris* type. This supposition was based on the following ratios: $F_2 = 21.9:1$ (including 2,540 plants); $F_3 = 4.67:1$ and 22.2:1. These were believed to represent 15:1, 3:1, and 15:1 respectively. The uniformity of the deviation from the expected ratios is believed not to be due to chance or to any failure of segregation, but to some modifying influence that perhaps prevented the development of certain combinations, as is supposed to be the case by Castle and Little (1910) in yellow mice and as has actually been observed in *Antirrhinum* by Baur (1910*a*).

SIZE DIFFERENCES.

From characters of form we come to those of size. The possible application to size of this theory of multiple factors so strongly indicated in color was recognized by Nilsson-Ehle (1907). He found that crosses of wheat and oats with long and short stalks gave intermediate hybrids whose offspring ranged all the way between the grandparents. The length of the head of wheat acted in crosses as though it were dependent upon a strong dominant-shortening factor and two similar weaker factors for length that lack dominance. For a normal head crossed with a *compactum* type (a special short head) gave a simple monohybrid ratio in F_2 of 3 *compactum* to 1 non-*compactum*. Yet a normal crossed with a very long type of head gave no grouping into two classes in F_2, but a continuous series of grades between the two grandparents, forming a frequency curve whose mode was intermediate.

Spillman (1902) has described fourteen crosses between wheats having long and short heads. F_1 gave intermediate heads. In F_2 "the progeny of each plant of the previous generation presented every gradation between the parents, forming a continuous series which, in most cases, extended beyond both parents." Crosses between strains of maize differing in the height of stalk have been made by Emerson (1910). Tall (225 cm.) × short (90 cm.) gave a uniform F_1 with a mean height of 182 cm. F_2 gave plants as small as the small parent and others taller than the first generation, but none as tall as the tall parent. One case is given (Emerson, 1911) of a cross between Missouri dent (tall) and a dwarf Tom Thumb pop, from which the F_2 generation had plants fully as tall and as short as the parents.

East and Hayes (1911) have described three crosses between varieties of maize with long and short ears which showed marked increased variability in the second generation. The distributions of the second generations include ears that are beyond the means of the parental races, whereas the F_1 ears (though large on account of increased vigor from the cross) do not approach the small parent. The standard deviations and coefficients of variability show this increased variability in every case. Crosses between races differing in the number of rows per ear were also made by East and Hayes; these gave increased variability in F_2. Five crosses gave similar results. A cross between two 12-rowed lines gave no increased variability in F_2. Similar results were found by Shull (1910 and 1911*a*) in comparable crosses. Two nearly pure selfed families had average variabilities of 9.08 and 9.06 per cent. The second generation of the cross had a variability of 12.63 per cent. This increase was said to be due to the existence of genotypic differences which appeared through the segregation of the different characters into different germ cells. This case is exactly like East's; and, although Shull does not mention Nilsson-Ehle in this connection, he has given good evidence for the belief in the existence of several factors that determine the number of rows.

Emerson (1910) reported three crosses between beans of different sizes in which an increased variability was found in F_2. The coefficients of variability in F_2 (based on sizes, weights, and shapes) are "usually twice and in some cases six or seven times as great as in F_1" (p.744). East and Hayes (1911) and Emerson (1910) have given cases of increased variability in F_2 from crosses between strains of maize differing in the size of grain. Crosses between strains of *Linum* which differed in the size of seed were studied by Tammes (1911). Length and width were investigated separately. Both showed constancy in an intermediate F_1 and variability in F_2. The range of variation transgressed the ranges of the parents, though the parental extremes were equaled only in rare cases. It was estimated (on the basis of the frequency of apparently pure parental forms in F_2) that four or possibly five similar independent Mendelizing units allelomorphic to their absence would explain the difference in variability in the first and second generations. Tammes (1911) found similar results in crosses between lines differing in the lengths and widths of petals.

The first experimental evidence of the appearance of increased variability in the size of animals after crosses is given in a preliminary report by Phillips (1912). Rouen ducks, whose average weights were, males 2,321 grams, females 2,244 grams, were crossed with mallards whose averages were, males 1,068 grams and females 928 grams. The F_1 average for 10 males was 1,665 grams; for 3 females, 1,587 grams; 33 F_2 ducks had averages a little higher. The coefficients of variability for the two generations were:

F_1 females = 3.43; males = 5.32. F_2 females = 11.07; males = 12.57

When classified in an absolute scale a similar increase in range was easily observed in F_2.

STRUCTURAL CHARACTERS.

Several structural characters have been found that seem to depend on two or more similar units. Of these the most important is the ligula in oats. Nilsson-Ehle (1909) made five crosses between varieties with and without ligulæ. In F_2 the following ratios were found; 4:1, 19:1, 44:1, 71:1, 274:1. The entire second generation of the cross that gave 19:1 was carried on to the next generation. The results found from this accorded very closely with the expectation, based on the assumption that the second generation ratio was due to the presence of two factors, each able to produce ligulæ. The higher ratios were believed to be due to three and four factors. In discussing this case Nilsson-Ehle says (1909, p. 85):

"Dieser Fall is also insofern von besonderem Interesse, als es durch denselben gelungen ist, das Prinzip von der Anwesenheit und Abwesenheit der Elementareigenschaften als Glieder je eines Merkmalspaares de facto auf ein Gebiet zu übertragen, wo man sonst nur per analogiam oder aus indirekten Gründen zur Annahme dieses Grundprinzips gelangen würde. Mit grösserem

Recht darf man wohl jetzt mit diesem Fall vor den Augen auch z. B. die Differenzen an Ährentypus beim Weizen und die darauf bezüglichen Spaltungen, ebenso wie die Spaltungen von Grösseneigenschaften usw. unter denselben Gesichtspunkt bringen. Die Theorie von der Gemeingültigkeit des genannten Prinzips und von der Bedeutung desselben zur Erklärung der von Mendel zuerst festgestellten und von den späteren Forschungen noch durchaus unerschütterten Gesetzmässigkeit, die sich in der Erzeugung der verschiedenen Gameten jedes Merkmalspaares in gleicher Anzahl aüssert, dürfte durch solche Fälle, nur noch fester begründet werden."

The spikelets in a head of oats may be arranged on all sides of the rachis, "Rispentypus," or all may be on one side, "Fahnentypus." Nilsson-Ehle (1909) has found (from crosses between varieties having these types of heads) that the Rispentype in five of eight crosses seemed to depend on one factor. The first generation gave an intermediate condition and three classes were found in the second generation in the ratio, 1:2:1. In some crosses the ratios showed that more than one factor was present determining the Rispentype. The Fahnentype appeared in the absence of factors producing Rispentype. Baur (1911, pp. 113–114) gives photographs of Nilsson-Ehle's plants, showing the various types of heads. Preliminary studies on the beard of wheat and waxy coating have been reported by Nilsson-Ehle (1908). He believes that both of these characters may be produced by two independent factors.

PHYSIOLOGICAL CHARACTERS.

Several physiological characters have been investigated by Nilsson-Ehle. These include winter hardiness, rust resistance, and time of flowering. Whereas there is little doubt as to the occurrence of increased variability in crosses differing in these characters, they have not been completely investigated. In lines of *Linum*, some seed capsules open when ripe, others remain closed. Tammes (1911) has made crosses between such lines and found that F_1 shows capsules half opened and that in F_2 there occurs a continuous series from the closed to the fully opened type.

Studies on the time of blooming of peas have been carried on by Tschermak (1911). Early blooming varieties crossed with late blooming varieties produce offspring with intermediate blooming times. The second hybrid generation shows great variability in the blooming periods; some plants were earlier than the early parent, others later than the late parent. The extremes inbred gave no intermediates, but remained true for early or late blooming, or were even more extreme than their F_2 parents. The intermediates in F_2 gave various results in the following generation. Some seemed to show segregation into two groups, others into three groups. So much is clear. Numerical ratios between three groups (early, middle, and late) were calculated. Those F_2 individuals falling within the ranges of the parental races grown in the corresponding years were called respectively early and

late, all the rest were classified as intermediate. On the basis of these results the following hypotheses were raised: There is a factor A which causes an intermediate blooming time, and a second factor B which in the presence of A makes the plant bloom much earlier. If each of these is allelomorphic to its absence and if dominance is lacking, the following theoretical formula would be expected:

3 early; 9 intermediate; 4 late.

By adding all the individuals in the corresponding classes in the second generations of all his crosses he obtains:

Observed: 60 early; 190 intermediate; 88 late.
Calculated: 63.3 early; 190 intermediate; 84.4 late.

In F_3 the expected segregation into 3 (intermediate):1 (late) was represented by 1.7:1; into 1 (early):3 (intermediate) by 1.2:1; and into 3 (early):9 (intermediate):4 (late) by 3:4.7:5. These agreements are not very close. The difficulty probably arises in the classification into the three groups. The hypotheses are complicated and largely depend on the arbitrary class limits.

Leake (1911) has presented studies upon the blooming time of cotton in much greater detail and with far greater numbers of individuals. Varieties that bloomed early were crossed with others that bloomed late. The hybrids were uniformly intermediate as to their blooming time, with no greater range than that of either parent. The second generation gave a much increased range. The frequencies formed a regular curve with the mode and mean nearer the late-blooming parent than the early parent, but none as late as the late parent. The time of blooming was shown to be very closely correlated with the type of branching. A monopodal plant blooms early; a sympodal plant blooms late. The hybrids were intermediate and in the second generation all degrees of branching, corresponding to the time of blooming, were found.

CROSSES BETWEEN SIMILAR LINES.

Perhaps as strong evidence for the assumption of different factors influencing the same character as is afforded by ratios in the second and third generations is found in crosses between forms apparently similar which give marked variability in F_2 after a uniform generation. The occurrence of two white races of sweet peas which give colored offspring when crossed is strong evidence for believing that two different factors are involved in producing color. In the following cases the factors are supposed to be of the same sort, so their presence can not be determined in F_1. Two strains of red wheat were found by Nilsson-Ehle (1911) which when crossed gave whites in the second generation. When two certain black oats were crossed, whites also appeared in the ratio of 15 blacks to 1 white. Two lines of oats (Nilsson-Ehle 1909) whose spikelets were arranged on all sides of the rachis (Rispentypus)

in F_2 gave some plants with spikelets all on one side (Fahnentypus). Kajanus (1911) reported three crosses between different long types of *Beta*, which gave similar forms in the first generation, while in the second generation very long individuals were obtained. Balls (1907), in crossing different strains of cotton with plants of the same height (60 cm.), found a great variability in the heights of F_2. F_1 was uniformly close to 100 cm.; F_2 ranged from 30 cm. to 100 cm., "although the plants had been practically level until two months old" (p. 365). Hayes (1912) has crossed varieties of tobacco with similar numbers of leaves which gave F_1 plants with the same number of leaves and F_2 plants with great variability in the number of leaves.

TRANSGRESSING SEGREGATION.

In certain cases quantitative morphological differences give imperfect monohybrid ratios; three classes corresponding to 1:2:1 may be found with every intergrade between them. In crosses involving different glume lengths in wheat Biffen (1905) found overlapping curves of this sort. Plants in F_2 with long and short glumes gave long and short glumes, respectively, in F_3, while intermediates gave all classes. Biffen also describes continuous multimodal curves of the F_2 frequencies from crosses of barley with heads of different lengths. Balls (1907) found a uniform F_1, taller than the tall parent, in a cross between cotton plants of different heights. The range of the second generation exceeded that of either parent and the frequency curve exhibited three modes, suggesting the monohybrid ratio. In crosses involving weight of seed he obtained bimodal curves in F_2. The seed weights in the parental lines were 0.10 grams and 0.125 grams; $F_1 = 0.155$ grams; $F_2 = 0.08 - 0.16$ grams. "Small seed segregates from large seed, and the segregated types show a greater range of fluctuation than is shown by either parent" (p. 372).

Another case of incomplete segregation into three classes is given by Leake (1911) in cotton leaves. The ratio of the width to the length of the central lobe of the leaf was called the leaf factor. For a race this leaf factor was found to be extremely constant. Crosses between races with different leaf factors gave intermediate offspring which were as uniform as either parent. (See a plate given by Allard, 1910). These inbred gave an increased variability in the leaf factor, forming a continuous series all the way between the extremes of the parents. The greatest frequency was half way between the original parents and at the mode of the first generation frequencies. But there were two lesser modes in the curve that corresponded to the modes of the parental frequencies. The ratio of individuals in these three groups was 1:2.2:1. The third generation showed that most of the individuals about the secondary modes remained within the parental ranges, while the plants about the large mode repeated the multimodal curve shown by the

second generation. It is remarked that these occurrences strongly suggest the results expected from a monohybrid Mendelian cross, although the occurrence of every intergrade between the two parents would not be expected. Shoemaker (1909) made crosses between cottons having different types of leaves. After an intermediate F_1, he obtained the three types in F_2 in the ratio of 1.27 : 2.73 : 1. The intermediates repeated this segregation in F_3, while the parental types bred almost true. This classification was made by inspection. From similar crosses of leaves Balls (1909) concludes that the leaf form is undoubtedly a compound character composed of several factors. In crosses involving wide and narrow central lobes he found no definite grouping in F_2, using statistical methods. Forms wider and narrower than the parental segments appeared, as well as intermediates. Some F_2 plants bred true.

It would be possible to compare these results with those of Nilsson-Ehle on the inheritance of the type of head in wheat. As stated above, the length of head is supposed to be influenced by a dominant unit (the *compactum* factor) whose presence is easily determined, and two weaker ones which lack dominance. There may be present in one of the cotton races one main unit without dominance, which influences the leaf factor and which is absent in the other race. This would account for the three modes in the second generation frequencies. There may also be present one or more weaker units also influencing the leaf factor, to whose segregation are due the sizes connecting the three curves and those few intermediates appearing when the extreme groups are inbred.

A case that may be described as due to one strong unit and one or more weaker ones is the inheritance of the size of plants in peas. Mendel (1865) considered the bush habit (he called it "dwarf") due to one dominant factor which, in crosses with long climbing plants, gave a regular 3:1 ratio. When tall bush and short bush lines are crossed an intermediate first generation results, followed in the next generation by the appearance of tall and dwarf bush plants with all intergrades. (Emerson, 1911, note 30, p. 88.)

That the interaction of two factors is necessary to produce color is a familiar conception. A color factor must be present before any factor due to produce a certain color can become active. An albino, then, may potentially have any color: it merely lacks the power to express color. Baur (1907) has given clear evidence that the various red colors of *Antirrhinum* are due to the action of certain factors, each of which, in the presence of all lighter factors, produces a certain shade of red. From this condition (which permits definite ratios) to one in which the different shades of a color can not be easily separated is not far. Tammes (1911) assumes a number of similar units that form the blue in her *Linum* races (see p. 11). Different combinations of these form a regular series of shades of blue. May it not be that the mono-

hybrid ratios obtained in crosses with white were due to the presence and absence of a color factor, as was suggested above? If this is at all correct a similarity is seen between this and the crosses in which factors of different strength affect the same character. The absence or presence of the strong color factor, a factor whose absence can not be questioned, makes the monohybrid ratio apparent, while the weaker factors for special color indicate their segregation by the new combinations and the new shades resulting from them.

SIZE CHARACTERS SHOWING MENDELISM.

Various cases will now be presented of the inheritance of size characters which appear to follow Mendelian expectations more closely than the preceding examples. A most instructive investigation on the inheritance of the height of peas has been presented by Keeble and Pellew (1910). Two semi-dwarf races of peas with very constant heights of 3 to 4 feet gave an F_1 of 7 to 8 feet. In F_2 plants were found ranging between 1.5 to 8 feet. This is very much like the cases cited above of crosses between strains having a similar character which becomes variable in F_2; but here the different factors that produce height have been more definitely analyzed. One parent had thick stems and short internodes; the other had thin stems and long internodes. In F_2 the tall plants had long internodes and thick stems, the short plants had short internodes and thin stems, while half the intermediates had long internodes and thin stems and half had short internodes and thick stems. Two characters tend to lengthen the plant; the internode length and the thickness (which was supposed to enable the internode to attain greater length). The ratios in the four classes closely approximated expectation. The classic case of tall-dwarf peas described by Mendel has been paralleled in other plants. Bateson and Punnett (1908) show that tallness and the unbranched habit in sweet peas are simple Mendelian dominants to dwarfness and the branched habit. The branched habit is dominant to the unbranched habit in stocks (Saunders, 1911). Emerson (1904) has shown that the axial position of the pods of beans is dominant to their terminal position. Tall and dwarf *Antirrhinums* act as a Mendelian pair (Baur, 1911). Tomatoes have dwarf varieties that have been demonstrated by Price and Drinkard (1908) to act as Mendelian recessives when crossed with normal lines. Salaman (1910) believes that length of the potato tuber is dominant to roundness. The long and short styles of *Oenothera* form a Mendelian pair (de Vries 1901, p. 435).

In animals the clearest cases of simple Mendelian inheritance in size characters are found in the long and short wings of *Drosophila* (Morgan, 1911) and in brachydactylous digits in man (Farabee, 1905, and Drinkwater, 1908). James Wilson (1909) shows that short stocky legs is a dominant character in the Dexter-Kerry breed of cattle.

The stature of man has been studied by Bean (1910) among Filipinos. He makes the following statements (p. 44):

"The study of the students by the method of grouping reveals types that apparently represent *character-complexes* composed of unit characters that obey Mendel's laws in heredity. A *character-complex* is a group of characters, such as the small stature, broad head, and broad nose of the Primitive, that hangs together in heredity or breaks up when crossed with another *character-complex*, such as the tall stature, long head, and long nose of the Northern, in the formation of new *character-complexes* which are recombinations in all possible ways of the individual characters, the original *character-complexes* being also retained."

Davenport (1911, pp. 42, 43) draws up the following laws of the inheritance of human stature, which suggest Mendelian phenomena at the bottom:

"The first general law is that, in case the four grandparents are very unlike, the adult children will vary greatly in structure, whereas when the grandparental statures are closely alike those of the children will be also. * * * The second general law is that when both parents are tall all of the children tend to be tall; but, on the contrary, if both parents are short some of the children will be short and some tall in ratios varying from 1 : 1 up to 2 : 1. If all of the grandparents are short then there tend to be twice as many short children as tall; but if one grandparent on each side be tall there will tend to be an equality of short and tall offspring."

SIZE CHARACTERS SEEMING TO "BLEND."

Although blending inheritance, in which offspring are always genetically intermediate between their parents regardless of the characters of their grandparents, has been generally believed to describe the phenomena observed in the inheritance of size characters, this is based on a small number of cases, none of which has been critically investigated. Very influential evidence in favor of the theory of blending inheritance has been the epoch-marking work of Sir Francis Galton (1889 and 1897) on human stature and Basset hounds. By studying pedigrees with statistical methods he arrived at his Law of Ancestral Inheritance, which Tschermak (1905) characterizes as follows:

"Die Grundidee der Galtonschen Lehre vom Ahnenerbe möchte ich dahin charakterisiren, dass die Eigenschaften der einzelnen Ahnen eines Individuums für dessen Aussehen in gesetzmässiger weise bestimmend sind. Es wird demnach—wenn ich so sagen darf—eine rein genealogische wertigkeit der einzelnen merkmale, je nachdem sie den vater oder der mutter, den Grosseltern oder noch ferneren ahnen zukamen, behauptet und zwar in einer gesetzmässig fallenden Progression." (Arch. f. Rassen u. Gesellschafts Biol., vol 2, 1905, p. 663.)

In the work with the pedigrees of the Basset hounds there is found a most surprising agreement between the facts and the results expected on the basis of this theory. The work of the school of statisticians founded by Galton and led by Pearson has been voluminous. It has undoubtedly revealed important facts about populations, racial tenden-

cies, and frequencies of characters, but it has not contributed to the biological understanding of these facts. Its laws are applicable to great masses of individuals from mixed matings, but they do not apply to individual pedigrees. They describe facts of inheritance mathematically instead of analyzing them biologically. And it is only by this latter method that the real mechanism of inheritance and of species formation can be finally revealed.

From a mathematical standpoint Brownlee (1911) has shown that the coefficients obtained by the statisticians would be expected in populations if stature, for instance, depends upon several independent Mendelizing factors. His conclusions are as follows:

> "(1) If the inheritance of stature depends upon a Mendelian mechanism, then the distribution of the population as regards height will be that which is actually found, namely, a distribution closely represented by the normal curve.
> "(2) There is nothing in the values of the coefficients of inheritance found by Sir Francis Galton and Professor Pearson which can not be explained on the basis of Mendelian inheritance." (Page 255.)

Lock (1906) states in general terms that crosses between corn strains of different heights gave an obviously intermediate first generation; that a number of these crossed back to the smaller parent gave a remarkably uniform generation, in which were found no signs of segregation into two groups, as should be expected if Mendel's law were to be applicable. He regards this condition as possibly due to a homogenous development of the germ cell. As no measurements were taken and as the number of individuals observed is not given, one may very well question the uniformity of this back cross. The work of Emerson stands in direct opposition to these results.

It is interesting to note that immediately preceding the discussion of height crosses, Lock describes the case of crossing dent and flint varieties of maize, which on similar evidence has been interpreted by East and Hayes (1911) as due to the action of two or more similar independent factors. This work was done by Lock before Nilsson-Ehle's discovery, so it was not even suspected that the great variability in the second generation might actually be due to segregation; instead, it was supposed that the occurrence of segregation could not be proved, as the variability masked its possible presence.

A far more exact and important investigation on a size character that was believed to "blend" in inheritance, is that of Castle and Walter (1909) on the length of rabbits' ears. Crosses between rabbits with long lop ears and with short erect ears gave offspring with intermediate ear lengths. These crossed with the long-eared parents produced a second generation with ear lengths intermediate between the F_1 and the long-eared parent; F_1 animals crossed with the short-eared parent gave a second generation with ears half way between these parents. Other crosses between crossed animals consistently gave

intermediates. The largest number of individuals from one pair of parents was 12; there were two fraternities of 9, while the average size of the thirty-five fraternities reported was 5.2 individuals. On the supposition that size differences are due to the presence of two or more similar independent activities, it would be impossible to find a marked difference in the variability of first and second generation fraternities consisting of five animals. If an intermediate F_1 animal from a cross involving three factor-differences for a size character be crossed back to one parent, there would be six intermediates to one like each parent. It is notable that with two of the largest fraternities given by Castle the variability is unusually wide. It is indicated that this variability is no greater than that found in the largest family of lops bred *inter se*. Three of these five lop-eared rabbits lie between their parents. The width of the range is then determined by two individuals. The curves plotted for these animals (Castle 1909, fig. 2, p. 13) show that at fourteen weeks one of these low animals had an illness, or was set back in some way, and at twenty weeks, when the records stop, it had not made up for this loss. The curves for ear growth and weight show the same thing. The second low animal at two weeks was only half as large as the other four, all of which were about the same size at that time. It has been found true of rabbits, as was noted in the case of cotton plants (Balls 1907) that the differences in size do not appear till several weeks after the birth. This means that normal curves of a litter would begin together and then fan out. (Compare curves given by Castle 1909, fig. 1, p. 11, and fig. 3, p. 15.) The curve of the rabbit in question remains below the others in that litter. In all probability this animal was set back seriously when first born and in fourteen weeks did not fully make up for it. Comparing the fraternity of twelve with the fraternities from short-eared rabbits bred *inter se*, and comparing it with the largest F_1 fraternities, its variability takes on a new light.

Since the appearance of Nilsson-Ehle's paper, Lang (1910), Baur (1910*b*), and Castle (1911), himself, have presented discussions of the possibility of finding increased variability in ear length in the second generation, among larger numbers of rabbits.

PART II.—EXPERIMENTAL.

INTRODUCTION.

In the following report of an investigation of the inheritance of the weight and of the size of various skeletal characters of rabbits, facts are presented that are believed to indicate an increase in variability as a result of size crosses. The work here described was started that further knowledge of the inheritance of the size of rabbits might be obtained, and, in the light of the evidence presented by Nilsson-Ehle, to test the hypothesis that differences in size may be due to the various groupings of similar independent Mendelian factors.

The original crosses of the large and small rabbits and the plan for breeding were made by Professor W. E. Castle in November 1908, who kept the records of their progeny until January 1910, when the investigation was put into my hands. With the exception of the recording of the weights during seven weeks in the summer of 1910, which was very generously done by Professor Castle, I have made all observations since 1909; I wish to acknowledge here a keen appreciation of my indebtedness to Professor Castle for the privilege of completing this work, which was already planned and started, and to express my deep gratitude for the untold assistance and advice that he has given freely during the course of these experiments.

ROLE OF ENVIRONMENT.

In any study of size or weight the control of food, temperature, and general surroundings is very essential. Valuable information on the actual influence of environment is given by a series of curves that have been made from a series of weighings of each animal (see p. 43). In the case of rabbits irregularities are very marked. Guinea pigs raised under identical conditions show much smoother curves. This difference may be due largely to the considerable mass of material constantly in the large cæcum of the rabbit, which is directly affected by any unfavorable condition that would cause a loss of appetite. So this cæcum would act as a magnifier of the actual fluctuations in the weight of the tissues themselves.

The rabbits were raised in two adjoining rooms, in which temperature and light conditions were similar. The rooms were heated by steam in winter and in summer were cooler than outdoors. The animals were all fed regularly on the same rations, with a change from fresh grass in summer to hay and mangels in winter. Oats were given them all

through the year. On account of a lack of room, guinea pigs were kept in the same pens with the rabbits that were not being bred. The normal pen held one rabbit and six pigs. This arrangement seemed to work very successfully. Certain rabbits would not live peaceably with certain pigs, but in such cases suitable changes were always made. Some growth curves show temporary losses due to hostile relations with pigs, but these cases are not numerous and complete recovery is found in every case.

While the health of the animals in general was very good, a disease known as "snuffles" was common. The symptoms of this are an apparent cold in the head and in many cases a sudden loss in weight, although many rabbits that showed the first symptom failed to lose weight. A study of the growth curves shows (see p. 43) that such abrupt losses were made up in the course of a few months. The presence of "snuffles" alone, then, did not seem cause for discarding an animal. When there was doubt as to the recovery of an animal, this one was not used. But such cases were very infrequent. In man most illnesses affect the body weight, but seldom is the ultimate weight or size changed thereby. The loss from sickness has been large. There have been recorded 364 individuals in back crosses to ♂2319. Of these 240 have been used. Besides such losses many animals not recorded died of infantile diarrhœa and coccidiosis, while numerous litters from first matings of F_1 animals were eaten by the mother.

The growth curves give ample evidence that each animal seemingly attempts to attain a certain weight; that, for losses due to any cause, there are subsequent compensating increases in the rates of growth, unless the animal does not recover. Minot (1891) arrived at a similar conclusion in his study of the growth of guinea pigs and he cites the case of childhood disease in relation to mature size. That the bones do not show such marked interruptions and variations in growth as the body weight is very apparent. Donaldson (1911) speaks of this as common observation. Careful studies of the growth of bones under favorable and adverse conditions have been carried on by Waters (1908). In cattle the height at the withers increases while the body weight is kept constant. This is even true for animals whose body weight is made to decrease. Curves of the increase in height of animals constantly gaining in body weight, of animals maintained at the same weight, and of animals constantly losing weight were parallel for four months. Then the rate of the increase in height of the animal losing weight began to fall off; this was followed in a month by the flattening of the curve of the animal maintained at a constant weight. In the light of these results it seems fair to believe that in the case of animals that have lost weight from any cause and made it up, the lengths of the bones have not been permanently altered.

The number of individuals in a litter might seem to influence the growth of the young at a critical period by the limit of the amount of milk received, but it is probable that there is a correlation between the production of milk and the number in the litter. If the sizes of the rabbits in different litters from the same parents are compared, different bones tell different stories. It may be noted, however, that when there are two litters of over four animals from the same parents their distributions are very similar for most characters. But even if rabbits of a large litter are under a disadvantage due to a scarcity of milk, we have seen that unfavorable conditions do not leave a permanent effect, and if the growth is slower at first it will be more rapid later when the animals eat the regular food, yet it may take several months for the animals to recover entirely; this is especially true of young animals. When the rate of growth is very rapid normally it takes longer for any loss to be repaired. To find a possible correlation between the size of the litter and the length of bones, averages of litters of four and less were compared with averages of litters of five and more (see table 1). In 12 litters of 4 and less were 42 rabbits; in 14 litters of 5 and more were 90 rabbits. The averages of a character for the large and for the small litters in each family were first found; then the grand averages of all the small and of all the large litters. In this way the different family sizes were taken into account. Grand averages were found for eight characters: five of these show the averages for the larger litters from 0.043 cm. to 0.002 cm. less than the averages of the smaller litters; one showed no difference; the other two gave averages for the smaller litters that were 0.044 cm. and 0.021 cm. less than the averages of the large litters (see table 1). The sum of the plus differences is 0.065, that of the minus differences is 0.087. Thus it is seen that there is no very marked difference that can be ascribed to the number in the litter.

TABLE 1.—*Comparison of large and small litters as regards average bone measurements.*

Measurement.	Litters of 4 or less.	Litters of 5 or more.	Difference of larger litters from smaller.
	cm.	*cm.*	*cm.*
O. M.	7.206	7.227	+.021
P. O.	4.377	4.375	−.002
P. M.	3.766	3.810	+.044
Za.	3.763	3.720	−.043
Te.	2.394	2.389	−.005
M.	3.570	3.557	−.013
H.	6.635	6.611	−.024
T.	9.601	9.601	0

The season of birth may be supposed to influence the early growth of the animals, but as the period of nursing is long this influence is probably very slight. Most of the animals were born between March and September; this probably has little significance, as the matings were

made when convenient, and in December there were several litters as large as those born in the summer. These experiments did not indicate that the mother's age had any influence.

The question of sex differences was investigated in the following manner: Litters with an equal number of males and females (or equal within one) were selected; the total number of males was 35, the total number of females 37; the averages of the measurements of the males were now compared with the averages of the same measurements for the females. The measurements of the males exceed those of the females in six cases; the reverse is true in ten cases. But the differences are not large and are probably without significance except in the four measurements in which alone they amounted to as much as a millimeter. These four measurements are P. O., P. M., F., and T.

TABLE 2.—*Comparison of males and females as regards average bone measurements.*

Measurement.	Males.	Females.	Differences of males from females.
	cm.	*cm.*	*cm.*
O. M.	7.388	7.389	−.001
P. O	4 411	4.557	−.146
P. M.	3.850	3.679	+.171
Za.	3.767	3.852	−.085
Zp.	4.038	4.069	−.031
Te.	2.426	2.425	+.001
Bc.	2.613	2.615	−.002
E.	2.464	2 475	−.011
N.	1 718	1.710	+.008
Na.	3.922	3.977	−.055
M_1	3 603	3.616	−.013
M_2	3.949	3 941	+.008
H.	6.720	6.727	−.007
U.	7.568	7.631	−.063
F.	8.407	8.015	+.392
T.	9 935	9 614	+.321

Apparently there is a difference between the two sexes in the position of the anterior margin of the palate, which lies farther forward in the females than in males. The difference amounts to about 1.5 mm. Consequently, in males the measurement P. O. is less than in females, and the measurement P. M. is greater, by about 1.5 mm.; the total skull length is substantially the same in both sexes.

The other apparently significant difference is in the long bones of the hind leg. In males the femur and tibia are 3 or 4 mm. longer than in females of the same size in other respects. This means that male rabbits have slightly longer hind legs than females.

The sexual differences in these four measurements amount to between 3 and 4 per cent, not enough to disturb materially the statistical results based on these measurements. In none of the remaining measurements can a sexual difference be detected.

Ample sources have been found for the origin of somatic or ontogenetic fluctuations. It will be shown now that there seems to lie behind these superficial changes, to which all the animals are equally subject, the deeper force of heredity determining the size attained by an animal, which produces (despite all possible vitiating influences) the constant difference that has been found in the variability of the two generations.

MATERIAL.

In the crosses to be described twelve rabbits were used as original parents. Two of these were males purchased from fanciers. There seems but little doubt that these came from fairly pure stock. One, a Himalayan, is from a race of small animals. As the Himalayan color pattern (white, with dark-colored ears, nose, feet and tail) behaves as a recessive to all other rabbit colors except that of the snow-white albino, there would seem to the fancier to be little advantage in outcrossing. The other male is a black-and-tan, a fairly recent variety of medium size, described by Castle (1909). Little can be said as to the purity of this animal. Since fanciers have definite standards of size for each variety there is strong probability that no wide crossing occurred in the pedigree of this animal. The remaining animals, ten females, were bred in this laboratory in connection with the investigations on the inheritance of ear length and color. They came from crosses of more or less diversity in size, although in no case was there a cross between animals with extreme weights, as is shown in tables 3*a*–*d*.

CROSSES.

The small Himalayan male (♂2319) was mated with each of the females. The female offspring (F_1) were bred back to the Himalayan, forming a back-cross generation. This was done on the theory that if any Mendelian phenomena were to take place, a greater number of segregates would have a chance to appear; for, on the basis of a one-character difference between the parents, the second generation obtained by breeding the F_1 hybrids together would give the recessive once in four, whereas in a cross between the F_1 hybrids and the recessive parent the two types would appear in equal numbers. Similarly, in crosses involving more characters, the back cross to the recessive parent would give a larger proportion of the recessive forms. In three cases F_1 males were crossed back to the large female parent. One cross ♀1493 × ♂2379, was used as a check; the weights of these animals may be given as 3,000 grams and 2,500 grams.

TABLE 3 A.—*Pedigree of* ♀ 1537.

The numbers in parentheses are weights in grams.

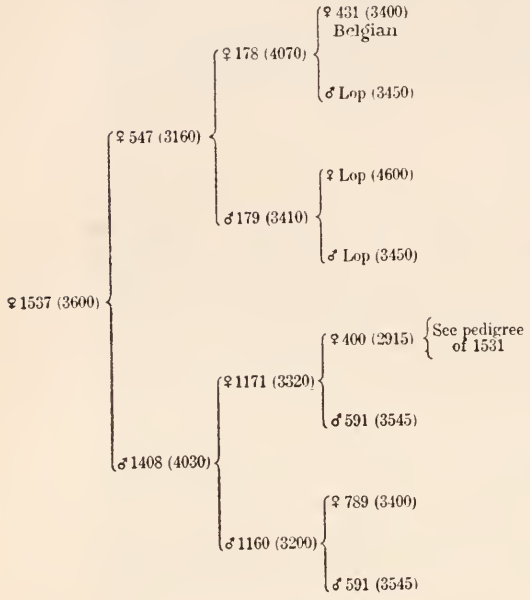


TABLE 3 B.—*Pedigrees of* ♀ *1493 and* ♀ *647.*

The numbers in parentheses are weights in grams.

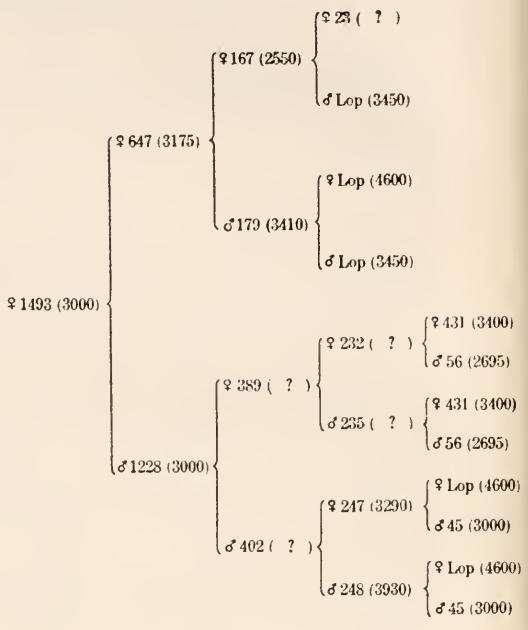


TABLE 3 C.—*Pedigree of* ♀ 1471.

The numbers in parentheses are weights in grams.

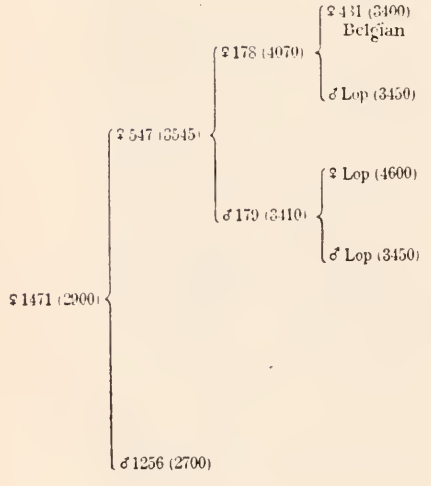
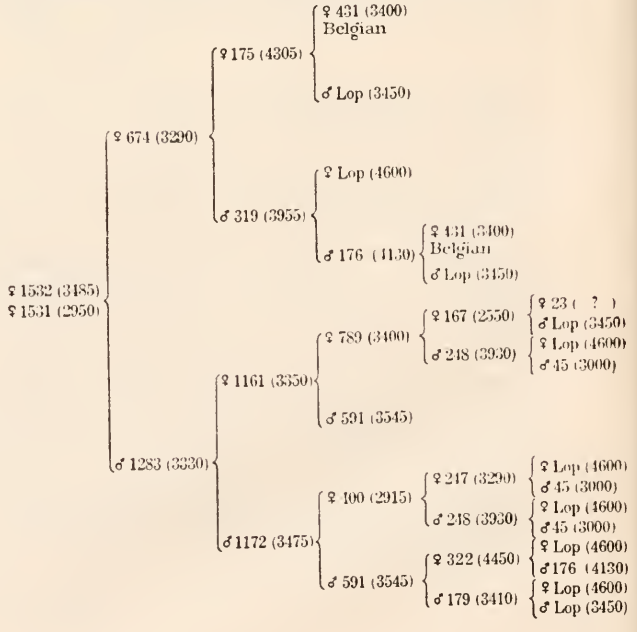


TABLE 3 D.—*Pedigrees of* ♀ *1531 and* ♀ *1532.*

The numbers in parentheses are weights in grams.



STUDIES OF SKELETAL MEASUREMENTS.

Prepared bones as a basis for the determination of the size of an animal have several advantages over living weight or any measurement taken on a living animal. They are practically unchanged by temporary unfavorable conditions or sickness; the adult size is simple to determine, whereas the body weight may be continuously increased by fat after maturity. Bone measurements are more analytical than weights; they can be more accurately measured and in cases of error or doubt may be remeasured at any time. They also offer material for further investigation, should a new theory or new method of comparison appear.

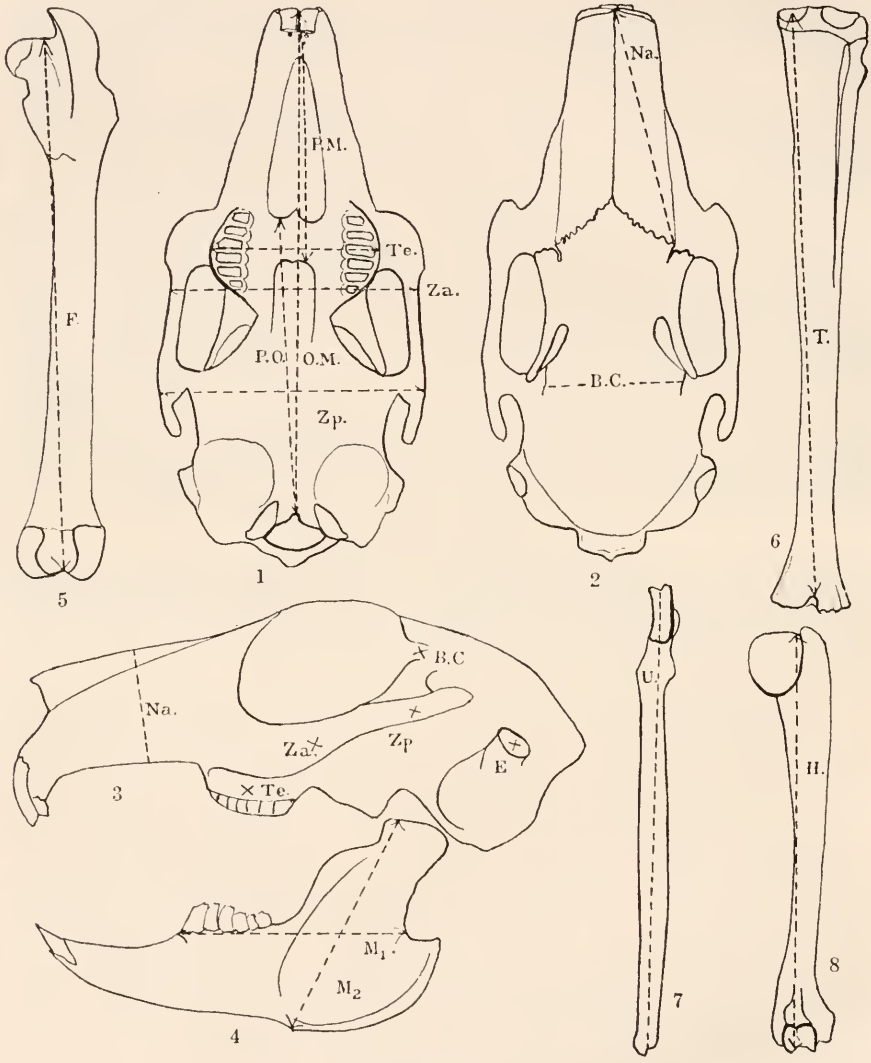
To ascertain the age at which bones stop growing, skeletons of rabbits of various ages were compared. Of the sutures destined to close completely, that between the proximal epiphysis and diaphysis of the humerus was found to be the last to close. By a study of this suture in humeri long boiled with "soapine," it was determined that ossification is completed by the twelfth month. Sexual maturity comes between the fifth and eighth months. To assure completed growth beyond all doubt, the animals were not killed until they were fifteen months old. In a few cases animals that died between twelve and fifteen months have been included, since by their measurements they were well within the range of others in the same fraternity.

MEASUREMENTS RECORDED.

From every animal the long bones of the right fore and hind legs and the skull were cleaned and saved. The following measurements were taken from these bones (compare figs. 1–8):

(1) From the anterior tip of the premaxilla to a median ventral notch in the basi-occipital on the margin of the foramen magnum (occipital to maxilla = O. M.).
(2) From the ventral notch in the basi-occipital to the anterior margin of the hard palate (palate to occipital = P. O.).
(3) From the anterior tip of the premaxilla to the posterior margin of the palate (palate to maxilla = P. M.).
(4) From the anterior to the posterior margin of the palate (palate = P.).
(5) The width of the zygomatic arch just behind the molar teeth (zygoma anterior = Za.).
(6) The width of the zygomatic arch just posterior to the pterygoid plates of the sphenoid (zygoma, posterior = Zp.).
(7) The width at third molar teeth, not including the zygoma (teeth = Te).
(8) The postorbital width of the brain-case (brain-case = Bc.).
(9) Width at the auditory meati (ears = E.).
(10) Height of skull anterior to molar teeth (nose = N.).
(11) The length of the nasal bone (nasal bone = Na.).
(12) The length of the mandible (= M_1).
(13) The height of the mandible (= M_2).
(14) The length of the humerus (= H.).
(15) Length of ulna (= U.).
(16) The length of the femur (= F.).
(17) The length of the tibia (= T.).

The measurements were taken with a pair of calipers provided with a vernier scale reading to tenths of millimeters. Repeated readings of the same measurement gave a constant observational error of 0.1 mm.



FIGURES 1–8.

Explanation of figures (reduced one-fourth from natural size).

1. Rabbit skull, ventral view.
2. Dorsal view.
3. Side view Crosses show ends of transverse measurements.
4. Mandible.
5. Femur.
6. Tibia.
7. Ulna.
8. Humerus.

STATISTICAL TREATMENT.

Coefficients of Variability Litter by Litter.

Coefficients of variability were calculated for each measurement in nearly all litters. (See table 4.) Being based on small numbers of observations, these coefficients show no uniformity, but they indicate that the different parts measured vary to some extent independently of each other. In some measurements a greater variability is found in a back-cross litter than in the F_1 generation in the same family, whereas in other measurements from the same sets of animals the F_1 generation may show greater variability; for instance, in family 647 the coefficient of variability for

Table 4.—*Coefficients of variability of the several litters of rabbits studied, in each of the seventeen measurements taken.*

Family.	Generation.	Number in litter.	O.M.	P.O.	P.M.	P.	Za.	Zp.	Te.	Bc.	E.	N.	Na.	M_1.	M_2.	H.	U.	F.	T.
647.....	F_1	4	2.7	5.1	2.3	0.2	2.3	2.6	1.3	2.2	1.8	2.0	6.6	1.1	2.5	5.9	1.6	1.2	1.8
	B.C.	6	4.0	3.8	5.1	0.5	3.6	3 5	3.5	1.3	1.3	3.8	4.7	2.6	2.5	3.1	2.1	2.6	2.8
	B.C.	4	2.6	2.7	3.4	0.2	2.7	1.8	3.6	0.5	3.8	5.1	3.3	1.5	1.8	2.7	2.0	3.1	2.6
	B.C.	7	2.5	3 4	2.4	0.3	2.8	1.9	2.8	3.9	2.1	8.7	3.5	2.3	3.5	2.5	2.5	2.9	3.1
1443.....	B.C.	6	2.6	2 8	2.1	0.4	1.5	2.0	2.8	3.0	1.2	2.5	3.4	1.8	2.1	1.1	1.5	1.2	1.0
1471.....	F_1	3	1.7	2.0	1.7	0.1	0.6	0.5	1.7	0.9	2.5	1.8	0.1	0.4	1.7	2.6	1.4	1.4	2.3
	F_1	4	1.4	1.4	2.2	0.3	1.3	1.5	4.8	1.3	3.6	2.6	3.7	0.6	1.3	1.3	1.9	1.8	1.6
	B.C.	7	2.6	2.3	2.1	0.7	1.5	2.6	1.1	3.0	1.2	5.0	3.4	1.8	3.4	1.7	2.2	2.1	1.5
1491.....	F_1	4	1.5	2.3	1.2	0.4	2.4	2.0	1.8	0.6	0.7	3.3	1.2	1.7	1.8	2.7	1.7	1.7	1.1
	B.C.	3	2.0	2.3	3.9	0.8	1.3	0.2	2.5	0.6	1.1	4.3	2.3	1.6	1.3	2.4	0.5	0.1	2.9
	B.C.	6	2.3	2.4	3.1	0.3	3.0	2.0	3.0	3.2	2.1	2.2	0.5	1.6	2.1	2.4	1.9	2.5	2.3
	B.C.	5	3 1	3.2	2.2	0.5	2.4	3.5	2.8	2.5	1.6	2.8	2.0	2.6	2.0	1.4	2.1	1.1	1.6
1493.....	F_1	7	0.7	0.8	1.6	0.4	1.7	0.5	2 4	1.1	1.2	2.7	2.3	1.5	2.4	1.3	0.6	1.4	1.4
	F_1	6	2.3	2.2	2.1	....	1.9	2.0	2.2	3.9	1.8	2.8	3.2	1.7	0.8	1.6	2.3	1.2	1.2
	B.C.	5	1.9	2.7	1.4	0.5	2.3	2.4	2.4	2.2	2.3	2.3	1.4	0.9	0.7	2.0	1.1	1.1	0.8
	B.C.	3	2.0	2.3	2.6	0.5	2.1	3.4	2.4	5.8	3.0	1.6	1.6	2.0	2.9	2.2	2.0	2.7	1.0
	B.C.	6	2.5	3.1	2.1	0.2	2.3	1.4	3.3	2.4	2.1	2.1	2.0	1.4	2.2	2.3	1.4	1.7	1.0
	B.C.	3	2.2	2.7	2.7	0.4	2 3	1.3	2.1	1.5	4.2	1.6	2.3	1.7	4.0	4.1	1.5	1.7	2.1
	B.C.	5	1.5	0.9	1.9	0.1	1.8	2.8	2.0	1.6	2.1	3.1	3.1	1.1	2.9	2.9	1.5	1.3	1.9
1531.....	F_1	2	1.0	1.5	0.7	0.5	1.7	0.4	0.3	1.3	0.5	0.5	1 3	1.1	0.8	0.2	0.1	1.0	2.4
	B.C.	6	1.6	1.6	1.0	0.3	2.4	3.1	2.6	3.1	1.8	2.9	3.0	1.4	2.0	3.4	2.7	3.4	3.2
	B.C.	4	4.3	1.2	5.4	0.7	4.7	3.3	5.8	3.2	5 2	6.1	5.9	4.3	5.5	5.0	3.8	4.9	4.0
	B.C.	8	1 9	2.2	3.0	0.7	1.3	2.3	1.2	2.6	2.6	3.7	3.2	1.6	0.7	2.7	1.7	2.5	2.1
	B.C.	4	2.8	3.3	3.5	0.3	2.2	2.0	2.0	2.0	2.5	3.3	5.2	3.0	3.2	3.6	2.1	2.1	2.9
1532.....	F_1	3	1.4	1.3	4.7	0.1	0.5	2.1	1.1	1.1	1.2	1.6	2.2	....	1.9	2.2	1.6	2.3	1.7
	B.C.	3	3.0	2.7	2.6	0.4	3.6	2.7	3.1	3.5	0.5	3.4	2.7	1.5	2.9	3.2	2.9	3.0	3.3
1537.....	F_1	2	3.4	3.4	2.9	0.5	1.1	0.2	0.3	1.4	0.3	5.4	0.9	1.0	1.9	6.5	4.0	3.6	5.2
	B.C.	9	3.2	3.6	5.1	0.5	1.4	2.0	2.2	1.4	3.4	4.8	3.0	1.5	3.1	2.4	3.4	2 7	2.9
	B.C.	4	1.5	1.4	.....	0.4	....	1.7	....	1.5	2.3	4.4	2.9	2.4	2.5	3.6	2.9	2.1	2.5
	B.C.	4	2.2	2.9	0.8	0.5	1.3	1.7	3.2	2.1	2.7	1.4	1.7	2.2	2.3	1.7	1.5	1.9	0.9
2011.....	F_1	2	1.6	2.3	2.1	0.0	1.2	1.7	0.1	2.2	1.1	2.1	1.9	1.1	1.7	4.9	1.9	0.7	1.3
	B.C	2	0.3	0.3	1.5	0.1	0.9	2.3	1.5	3.3	2.8	2.9	1.0	1.1	2.6	0.0	3.1	1.5	3.4
	B.C.	3	1.3	2.3	2.2	0.2	1.1	0.7	2.2	....	0.0	0.2	1.2	2.4	2.7	2.1	3.3	....	0.5
	B.C.	5	2.4	5.5	2.0	0.9	2.2	3.8	2.1	3.1	2.5	3.7	2.3	2.2	2.0	1.1	1.0	1.5	1.2

P. O. in generation F_1 is 5.1, while in the back-cross litters it is 3.8, 2.7, and 3.4; in the same family the coefficients of variability for Te. are: $F_1 = 1.3$, back-cross $= 3.5$, 3.6, and 2.8. Similarly the measurements Na. and H. show coefficients for F_1 larger than any for the back-crosses, and Za., N., M., U., F., T. have coefficients of variability for F_1 smaller than any for the back-crosses. The coefficients of F_1 for the other ten measurements are within the range of the back-cross coefficients. The other families all show similar irregularities.

Coefficients of Size.

In order to get a clearer view of the variabilities treated in table 4 and to study variability by comparing whole animals instead of their parts, it seemed desirable to find a coefficient for each individual that would express the average of the sizes, or of the deviations of its different parts. As the measurements range from 2 to 10 cm., no absolute average of deviations could be used, for a small deviation in a short measurement would have far greater significance than an equal deviation in a long measurement and so, in any average, the large deviations in a long measurement would entirely overbalance the equally important small deviations in short measurements.

The following method based on relative deviations was employed to obtain coefficients of size (C. S.) for each animal. The average of a character for one fraternity was used as a dividend into which were divided the individual measurements of the animals in the same fraternity. The quotients so found gave a series of ratios expressing the relative sizes of the various sibs above or below their mean. An animal with a character at the mean would have a ratio of 1 for that character; an animal whose measurement was shorter than the mean would have a ratio above 1; an animal with a measurement above the mean would have a ratio below 1. By this method the ratios of all the characters of one animal to the corresponding fraternal means were obtained. The average of these ratios gave the coefficient of size (C. S.) for that animal.

In order to avoid giving too much importance to one dimension of the skeleton and to escape errors occasioned by using characters unequally subject to errors in observation, not all measurements were included in calculating these coefficients of size. The second and third measurements on the skull, P. O. and P. M., being functions of the total skull length, were not used. The width of the palatine bridge (P.) was too small to show any easily determinable variation. Only one zygomatic width was included (Za.). The widths of the skull at the teeth (Te.), the brain case (Bc.), and the ears (E.) are generally very similar. As the width of the brain case in animals with very long skulls is often less than that of intermediate skulls, and as the measurement at the ears is liable to larger errors in observation than the width of the teeth, this last character (Te.) alone was used. The anterior height of the skull (N.) is a short measurement and is as much influenced by the degree of convexity of the nasal bones as by any variation in bone size. The length of the nasal bone being limited at one end by an extremely irregular dentate suture is unsatisfactory in spite of its length. Lists of the characters used and those not used in determining coefficients of size are given herewith.

Characters used.	Characters not used.
O. M.	P. O.
Za.	P. M.
Te.	P.
M_1.	Zp.
M_2.	Bc.
H.	E.
U.	N.
F.	Na.
T.	

The standard deviations of the coefficients of size were calculated for each fraternity. Since the coefficient of size is the expression of a relation between measurements in one animal and corresponding means in its fraternity, coefficients of size in different fraternities of the same family may be treated together. The standard deviations found by such combining will be based on deviations from the various fraternal means. This will give a fairer result than if the actual deviations had been calculated from the means of all the individuals averaged together, as would naturally be done in determining the standard deviation of a whole generation. It is supposed that the means of the fraternities are not just the same. A common mean would give the extreme variates even greater deviations and the standard deviation would be higher than the deviation obtained by the method presented here. It will be seen now that the coefficients of size for fraternities of the same generation in different families may be treated together, for in the coefficients of size 1 always stands for the mean, whatever the actual value.

In table 5 these frequencies are classified in classes 0.005 in extent. The row of numbers at the top is the scale of coefficients of size; each number represents the lower limit of its class. On the left are given the family numbers, the generation, F_1, or back-cross to the male (BC), with the ledger numbers of the F_1 females that were back-crossed. On the right are given the standard deviations, in terms of the ratios, for the frequencies shown on the same horizontal line. From the distributions themselves, it is clearly seen that in families 647, 1491, 1493, and 2011 the F_1 fraternities are less variable than the corresponding back-crosses, whether the latter are taken together or separately. The standard deviations show the same facts in a more concise form.

In families 1493×2379, 1531, 1532, and 1537 the F_1 generations contained less than four individuals, so the coefficients of size and the standard deviations were not found. The standard deviation of these back-crosses can be compared with the standard deviations of the back-crosses and F_1 generations in other families. The back-crosses of families 1531 and 1532 have standard deviations considerably larger than the largest F_1 standard deviation. In families 1537 and 2037 standard deviations of the back-crosses are only a little larger than the largest F_1 standard deviation. The standard deviation of the total back-cross frequencies in 1493×2379 is less than the largest F_1 standard deviation.

It must be noted here that this family was raised for a check, as the difference between the parents is very small. When the coefficients of size of all the first generations are used together the standard deviation, based on 33 individuals, is 0.0143. When the coefficients of size of all the back-crosses to the male (excluding the check-cross, 1493×2379) are calculated together the standard deviation, based on 240 individuals, is 0.0232. Whether taken by single fraternities, by families, or by generations, there is a greater variability in all the crosses back to the male than in the F_1 generation.

TABLE 5.—*Coefficients of size for the offspring studied, arranged by families, together with the standard deviations for size in the several families.*

The abbreviation B. C. means back-cross.

Family.	Generation.	F¹ mother.	.930	.935	.940	.945	.950	.955	.960	.965	.970	.975	.980	.985	.990	.995	1.000	1.005	1.010	1.015	1.020	1.025	1.030	1.035	1.040	1.045	1.050	1.055	1.060	1.065	Standard deviation.
647	F_1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	2	.....	.....	1	.....	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0145
	B. C.	2411	.....	.....	.....	.....	.....	.....	1	.....	1	1	2	.....	.....	.....	1	.....	1	.....	1	1	.....	1	.....	.....	.....	.....	.....	.....	.0251
	B. C.	2474	.....	.....	.....	.....	.....	.....	1	.....	.....	.....	1	1	.....	.....	1	.....	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0214
	B. C.	2475	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....	1	1	1	.....	1	1	1	.....	1	.....	.....	.....	.....	.....	.....	.....	1	.0336
	B. C.	Totals	.....	.....	.....	.....	.....	1	2	1	1	1	3	2	1	1	2	1	2	1	2	2	.....	1	.....	.....	.....	.....	.....	1	.0277 ± .0026
1443	B. C.	2537	.....	.....	1	.....	.....	1	.....	1	2	.....	.....	.....	3	1	1	1	.....	2	2	1	.....	.....	.....	.....	1	.....	.....	.....	.0262 ± .0033
1471	F_1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	2	.....	1	1	.....	.....	.....	1	1	.....	.....	.....	.....	.....	.....	.....	.....	.0154
1491	F_1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	.....	.....	1	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0148
	B. C.	2407	.....	.....	.....	.....	.....	.....	.....	1	2	.....	1	1	1	2	2	2	1	1	1	1	1	.....	.....	.....	.....	.....	.....	.....	.0193
	B. C.	2408	.....	.....	.....	.....	.....	.....	.....	.....	1	1	.....	.....	.....	1	1	.....	1	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0175
	B. C.	Totals	.....	.....	.....	.....	.....	.....	.....	1	3	1	1	1	1	3	3	2	2	3	1	1	1	.....	.....	.....	.....	.....	.....	.....	.0183 ± .0013
1493	F_1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	3	.....	2	2	4	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0094
	B. C.	2519	.....	.....	.....	.....	.....	.....	.....	1	2	1	1	4	1	2	2	1	.....	1	1	.....	.....	1	.....	.....	1	.....	.....	.....	.0216
	B. C.	2520	.....	.....	.....	.....	.....	1	.....	1	.....	.....	.....	1	.....	1	3	.....	3	1	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0176
	B. C.	2523	.....	.....	.....	.....	.....	.....	1	.....	.....	.....	1	2	2	2	3	1	2	.....	1	1	.....	.....	.....	.....	.....	.....	.....	.....	.0164
	B. C.	2526	.....	.....	.....	.....	.....	.....	.....	1	1	.....	.....	1	.....	1	2	2	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0178
	B. C.	3057	.....	.....	.....	.....	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	1	1	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0204
	B. C.	Totals	.....	.....	.....	.....	.....	1	2	.....	3	1	2	8	3	6	11	5	6	2	4	1	.....	1	.....	.....	1	.....	.....	.....	.0207 ± .0013
	F_2	.....	.....	.....	.....	.....	.....	.....	2	3	1	.....	2	.....	.....	.....	1	1	.....	.....	1	1	.....	.....	.....	.....	.....	.....	.....	1	.0314
1531	B. C.	2388	1	.....	.....	.....	.....	1	1	.....	1	1	4	1	1	1	4	1	1	2	2	1	1	2	.....	.....	.....	1	.....	.....	.0274
	B. C.	2389	.....	.....	.....	.....	1	.....	.....	1	1	.....	3	.....	3	2	2	.....	1	.....	1	1	.....	.....	1	.....	.....	1	.....	.....	.0251
	B. C.	Totals	1	.....	.....	.....	1	1	1	1	2	1	7	1	4	3	6	1	2	2	3	2	1	2	1	.....	.....	2	.....	.....	.0265 ± .0017
1532	B. C.	2396	.....	.....	.....	1	1	.....	2	1	1	1	.....	1	1	.....	.....	2	1	.....	2	1	.....	.....	.....	.....	.....	.....	.....	.....	.0263 ± .0031
1537	B. C.	2398	.....	.....	.....	.....	1	.....	1	.....	1	1	2	.....	.....	5	2	3	2	2	.....	2	.....	.....	1	.....	.....	.....	.....	.....	.0207
	B. C.	2399	.....	.....	.....	.....	1	.....	.....	.....	1	2	1	1	1	3	2	2	.....	3	2	.....	2	.....	.....	.....	.....	.....	.....	.....	.0196
	B. C.	Totals	.....	.....	.....	.....	2	.....	1	.....	2	3	3	1	1	8	4	5	2	5	2	2	2	.....	1	.....	.....	.....	.....	.....	.0202 ± .0013
2011	F_1	.....	.....	.....	.....	.....	.....	.....	1	.....	.....	.....	.....	.....	.....	1	1	1	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0187
	B. C.	2536	.....	.....	.....	.....	2	.....	.....	.....	.....	.....	.....	.....	.....	3	1	.....	1	.....	2	.....	1	1	.....	.....	.....	.....	.....	.....	.0254 ± .00386
1493 × 2379	B. C.	2453	.....	.....	.....	.....	1	.....	.....	1	.....	.....	.....	1	.....	2	.....	2	5	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.0187
	B. C.	2452	.....	.....	.....	.....	.....	.....	.....	.....	1	3	.....	2	.....	2	2	1	1	4	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	.0166
	B. C.	Totals	.....	.....	.....	.....	1	.....	.....	1	1	3	.....	3	.....	4	2	3	6	6	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	.0174 ± .0015
F_1 totals, all families			.....	.....	.....	.....	.....	.....	1	.....	.....	.....	3	7	2	4	5	5	1	1	3	1	.....	.....	.....	.....	.....	.....	.....	.....	.0143 ± .0011
B. C. ♂ totals, all familes except control 1493×2379			1	.....	1	1	6	4	8	8	14	8	16	14	17	23	27	18	15	17	16	11	5	4	2	.....	2	2	.....	1	.0232 ± .0007

Classification in Relation to Parents.

Using coefficients of size gives no information as to the relative sizes of the parents and the two following generations. To show this and to indicate the comparative distributions of the frequencies of the two generations based on actual measurements, a table has been formed in which the rabbits are classified one character at a time in regard to their size as compared with their two parents. See table 7, pages 40 and 41. Only crosses with ♂2319 and the subsequent back-crosses have been used in this tabulation. The difference between a pair of parents in the size of a character was divided by 16. This gave the width of one class for this character in this family. By calling the parents the means of two extreme parental classes there remained fifteen equal classes between them. The measurements of the same character in all the F_1 and back-cross animals from these parents were arranged in classes, whose limits were determined in this way. Similarly each family was classified for this character. From tables so formed the number of animals in all families that fall half way between their parents in regard to this character is readily found by adding the frequencies in the middle column; and so the sums of the frequencies in the other columns show the distribution of animals in other relations to their parents. The sums of all the F_1 animals in the various classes were plotted in a frequency curve; the sums of the back-cross classes were plotted in a comparable curve. By this same method the other characters were classified and curves plotted, showing the positions of the F_1 and back-cross animals in relation to their parents or grandparents (see fig. 9, page 42). In table 7 the offspring are grouped with reference to the measurements of the parents of the family; the measurement of the father falls in the middle of class 1 in every case, and that of the mother in the middle of class 17. Between these two classes lie fifteen classes in which a majority of the offspring occur, though it will be observed that some of the offspring exceed the mother's measurement (class 17), falling in classes 18 to 25, while others fall below the father's measurement (class 1) and so are found in classes -1 to -13. The correspondng generations of the several families are combined, class by class, to form grand totals as regards each measurement taken.*

In general it may be said of all the characters that the intermediate size of the greater number of the first generation is very apparent. If they occupied an exact middle position between their parents, their mean would in every case fall in class 9. In two measurements, *Na.* and M_2, this condition is practically realized (see table 6); in one measurement, *Za.*, the mean lies nearer to class 8 than class 9—that is, the F_1 offspring fall slightly below the intermediate class; but in all the other measurements, they are from one to three classes higher than the intermediate

*With the assistance of Mr. S. Wright means and standard deviations were calculated for the F_1 offspring and the offspring from the back cross with the father, as given in table 6.

class. This tendency of F_1 offspring to exceed the midparental measurements (class 9) may readily be interpreted as the effect of increased vigor in consequence of the cross. It does not persist in the back cross, or in F_2. East (1909) and Shull (1909) have shown that hybridization may cause an increased stimulus to cell division, which has no relation to inheritance. The classic work of Darwin (1876), that showed the increased size of crossed over self-fertilized plants, may also be cited.

Perhaps the most surprising fact shown by the distributions of the first generation is the occurrence of individuals, some of whose parts are almost as small as those of their small parent and others with measurements larger than those of their large parent. This does not mean that any F_1 animal was, as a whole, as extreme as its parents. A marked difference in variability is seen when curves for different characters are compared. When the range is wide it is as much extended in one direction as in the other. Such a difference is found when the curve for the ulna (U.), which has a very wide range, is compared with the curve of the skull length (O. M.), which has a very limited range; yet these curves are based on the very same individuals. With narrow ranges comparable to that of the skull length are the curves for the two partial skull lengths (P. O. and S. M.) and the mandible measurements (M_1 and M_2); but the width at the teeth (Te.) and the anterior zygomatic width have wider ranges. The posterior width of the zygoma (Zp.), the length of the nasal bone (Na.), and the four leg bones (H., U., F., T.) all show still wider ranges.

Pearson (1902, p. 378) found similar inequalities in the different parts of the human body:

> "The inheritance of all characters does not appear to be the same. The inheritance of forearm is for all four cases sensibly less than the inheritance of span, and that of span less than that of stature."

Hatai (1907) found greater variability in the length of the nasal bone and the zygomatic width in skulls of albino rats than in any other skull characters.

The above discussion on the ranges in different characters based on the curves of the first generation applies equally well to the curves of the back-crosses. If the offspring from a back-cross with the father occupied the middle class between the midparental for F_1 and the class for the father, they would fall in class 5. In four measurements (see table 6) the means fall approximately in class 5, namely, the skull length measurements (P. O. and S. M.), the mandible measurement (M_2), and the ulna measurement (U.). Of the remaining measurements, five lie nearer class 6 than class 5—that is, exceed expectation by one class—while four lie nearer class 4 or lower classes with an average deviation of about two classes. The deviations are pretty evenly divided between plus and minus with reference to class 5. This is what would be expected on a theory of blending inheritance, but also on a theory of Mendelian

inheritance involving multiple factors without dominance. However, a very marked feature of the frequencies of the back-cross offspring is the number of measurements that are as low as and lower than the small parent and as high as and higher than the modes of the F_1 curves in which their mothers are recorded. Since the father and grandfather in all these families were the same rabbit, the actual values of classes near his class in different families are very nearly the same. All animals that fall in his class have the same size as he, and those that fall in an adjacent class are of nearly the same absolute size as compared with each other. This makes the occurrence of these short measurements the more convincing evidence of segregation. The standard deviations of the F_1 and back-cross generations given in table 6 are further evidence of segregation, in that they show that in general the variability of the back cross is greater than that of F_1 while taking into account the differences in numbers in the two generations. In six measurements (O. M., S. M., Zp., T., M_1., M_2) the standard deviation of the back-cross offspring is significantly greater; in three measurements (Na., U., F.,) it is significantly less. In the four other measurements (Za., P. O., H., T.) the difference lies within the probable error and so is not significant.

TABLE 6.—*Means and standard deviations of the F_1 and back-cross generations, based on the classifications given in table 7 and expressed in terms of those classes.*

Measurement.	Mean F_1.	Mean B. C. ♂	ρ F_1.	ρ B. C. ♂
O. M.	10.80	5.55	1.94±.15	2.60±.08
P. O.	10.56	5.24	2.76±.21	2.69±.08
S. M.	10.02	5.28	2.50±.19	2.80±.09
Za.	8.39	2.01	3.17±.24	3.52±.11
Zf.	11.00	2.17	3.63±.27	4.58±.14
Te.	10.12	5.69	2.56±.19	2.88±.09
Na.	9.20	4.35	3.47±.26	2.87±.09
M.	10.27	4.75	2.04±.15	2.99±.09
M_2	8.95	3.16	2.90±.22	3.29±.10
H.	12.20	5.86	3.65±.27	3.55±.11
U.	12.24	5.27	5.43±.42	4.61±.15
F.	11.83	5.54	3.85±.30	3.38±.10
T.	11.90	6.16	4.67±.31	3.98±.12

SUMMARY.

Studies of bone measurements have shown that there is greater variability in the second generation from a size cross than in the first. This is shown by the use of coefficients of size in which the different measurements for one animal are expressed, as well as by the classification of the two generations (one character at a time) in relation to their parents. Numerous individuals are found in back crosses with measurements as short or shorter than the corresponding measurements in the small parent; others are found with parts larger than the corresponding modes of the first generation. The standard deviations of the grand totals of these classifications indicate an increase in the back cross in about half of the measurements.

TABLE 7.—*Classification of the F_1, F_2, and back-cross (B. C.) rabbits*

[B. C. ♂ means offspring of a back-cross with the father; B. C. ♀ means

Measurement.	Generation.	Class No.																		
		−13	−12	−11	−10	−9	−8	−7	−6	−5	−4	−3	−2	−1	0	1	2	3	4	5	6
O. M.	F_1																				
	F_2														1					1	4
	B. C. ♂													3	6	4	13	18	42	32	38
	B. C. ♀																				
P. O.	F_1																1				1
	F_2												1					2	1	2	
	B. C. ♂											1	3	2	3	9	15	21	38	39	30
	B. C. ♀																				
S. M.	F_1																				2
	F_2														1					4	2
	B. C. ♂											1	1	2	5	9	18	19	40	41	36
	B. C. ♀																				1
Za.	F_1																1	1	1	5	2
	F_2							1						1	1	1	3	1	1		2
	B. C. ♂						1	2	1	2	6	11	15	22	19	27	32	24	20	15	12
	B. C. ♀																		2		2
Zp.	F_1																	1		1	
	F_2										1				1		1	2	1	1	1
	B. C. ♂				1		1	5	3	9	11	7	13	15	27	17	15	22	20	20	14
	B. C. ♀																			1	
Te.	F_1																			1	2
	F_2															1	1		2	1	
	B. C. ♂													5	2	8	13	28	35	26	22
	B. C. ♀																				1
Na.	F_1																1			5	6
	F_2													1		2	1		1	3	3
	B. C. ♂												2	8	7	16	25	44	35	34	18
	B. C. ♀																			1	
M_1	F_1																				1
	F_2																1			1	5
	B. C. ♂										1		6	5	2	11	14	36	42	30	34
	B. C. ♀																				
M_2	F_1																			4	8
	F_2												1	2	2	1	1	1			1
	B. C. ♂								2	1	5	7	3	7	24	18	29	35	24	31	18
	B. C. ♀																	1		2	
11.	F_1																1			1	
	F_2														1		1			4	1
	B. C. ♂								1				3	4	5	8	17	20	28	25	29
	B. C. ♀																				
U.	F_1													1		1			2		1
	F_2	1										1	1				1	4	2	1	
	B. C. ♂						1		2	3	1	2	4	4	12	11	29	26	17	19	18
	B. C. ♀											1					1				1
F.	F_1																1				2
	F_2										1				1		1	1	3		1
	B. C. ♂										1	1		1	4	6	7	16	26	34	27	26
	B. C. ♀																				
T.	F_1																	1	1	2	
	F_2											1			1		1		2		1
	B. C. ♂								1	1	1		1	4	4	12	13	24	32	14	21
	B. C. ♀																				1

as regards each measurement, in relation to the measurements of the parents.

offspring of a back-cross with mother. Parental classes are in heavy ruling.]

Class No.																			Generation.	Measurement.
7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		
2	2	8	5	10	7	3	2	2	....	....	....	....	....	....	....	....	....	....	F_1	O. M.
1	1	1	2	2	1	....	....	....	....	....	....	....	....	....	....	....	....	....	F_2	
34	16	16	8	4	3	1	....	....	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
....	....	2	....	4	2	2	4	3	1	....	....	....	....	....	....	....	....	....	B. C. ♀	
2	5	4	6	8	6	4	1	....	2	1	....	....	....	....	....	....	....	....	F_1	P. O.
....	3	1	3	....	1	....	....	....	....	....	....	....	....	....	....	....	....	....	F_2	
32	18	16	5	....	3	2	....	....	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
....	....	1	....	4	4	1	2	3	2	1	....	....	....	....	....	....	....	....	B. C. ♀	
6	3	7	7	7	3	2	1	2	....	1	....	....	....	....	....	....	....	....	F_1	S. M.
2	1	1	1	1	....	1	....	....	....	....	....	....	....	....	....	....	....	....	F_2	
22	15	15	7	3	2	2	2	....	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
....	....	....	3	5	2	3	2	....	1	....	1	....	....	....	....	....	....	....	B. C. ♀	
9	4	5	3	2	4	2	....	1	....	1	....	....	....	....	....	....	....	....	F_1	Za.
2	1	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	F_2	
12	12	3	3	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
....	2	....	4	2	2	1	1	2	....	....	....	....	....	....	....	....	....	....	B. C. ♀	
3	5	6	2	6	6	2	1	1	3	2	....	....	....	....	....	....	....	....	F_1	Zp.
1	1	1	....	....	....	2	....	1	....	....	....	....	....	....	....	....	....	....	F_2	
13	4	10	2	5	3	2	....	1	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
....	1	1	....	2	2	3	1	1	1	....	1	....	1	1	1	....	1	....	B. C. ♀	
6	3	5	4	5	8	4	2	....	1	....	....	....	....	....	....	....	....	....	F_1	Te
1	2	....	2	1	1	1	....	1	....	....	....	....	....	....	....	....	....	....	F_2	
37	24	18	10	3	5	3	....	....	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
1	1	....	1	2	3	1	3	3	1	1	....	....	....	....	....	....	....	....	B. C. ♀	
4	3	3	5	3	2	4	....	4	1	....	....	....	....	....	....	....	....	....	F_1	Na.
2	1	2	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	F_2	
15	14	11	4	2	3	2	....	....	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
1	....	1	2	2	2	4	3	....	....	....	1	....	....	....	....	....	....	....	B. C. ♀	
2	6	6	8	6	7	2	2	1	....	....	....	....	....	....	....	....	....	....	F_1	M_1
1	1	....	2	....	1	1	....	....	1	....	....	....	....	....	....	....	....	....	F_2	
25	11	10	5	4	....	1	....	....	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
....	2	1	4	1	2	3	1	2	....	....	1	1	....	....	....	....	....	....	B. C. ♀	
4	3	6	4	2	4	2	3	1	....	....	....	....	....	....	....	....	....	....	F_1	M_2
3	....	....	1	....	....	1	....	....	....	....	....	....	....	....	....	....	....	....	F_2	
13	10	5	2	3	....	....	1	....	....	....	....	....	....	....	....	....	....	....	B. C. ♂	
....	....	1	4	2	3	2	....	1	....	....	1	1	....	....	....	....	....	....	B. C. ♀	
....	2	5	6	....	4	7	6	3	1	1	1	1	....	....	1	....	....	....	F_1	H.
1	2	2	....	1	....	....	1	....	....	....	....	....	....	....	....	....	....	....	F_2	
30	23	11	14	5	8	3	2	....	....	2	1	....	....	....	....	....	....	....	B. C. ♂	
....	....	1	1	3	....	3	1	2	3	3	....	....	....	....	....	....	....	....	B. C. ♀	
1	1	2	2	5	3	1	7	3	2	1	....	....	....	2	....	1	....	1	F_1	U.
....	....	....	....	2	....	....	....	....	....	....	1	....	....	....	....	....	....	....	F_2	
15	12	13	15	11	5	2	4	2	2	....	....	1	1	....	....	....	....	....	B. C. ♂	
....	1	1	....	1	1	1	1	1	1	....	....	....	2	1	....	1	....	3	B. C. ♀	
1	3	2	7	2	8	3	5	1	2	2	....	....	....	1	....	1	....	....	F_1	F.
....	2	....	1	1	1	....	1	....	....	....	....	....	....	....	....	....	....	....	F_2	
30	15	13	10	7	5	2	2	....	....	1	1	....	....	....	....	....	....	....	B. C. ♂	
1	1	1	....	3	....	1	1	3	3	....	1	1	2	....	....	....	....	....	B. C. ♀	
3	1	2	2	4	7	2	6	2	3	1	1	....	1	1	....	....	....	....	F_1	T.
1	3	....	2	....	....	....	1	....	1	....	....	....	....	....	....	....	....	....	F_2	
29	18	17	11	13	10	4	1	2	4	....	....	....	1	....	....	....	....	....	B. C. ♂	
....	....	1	....	....	1	1	....	4	1	1	2	1	2	1	....	2	....	....	B. C. ♀	

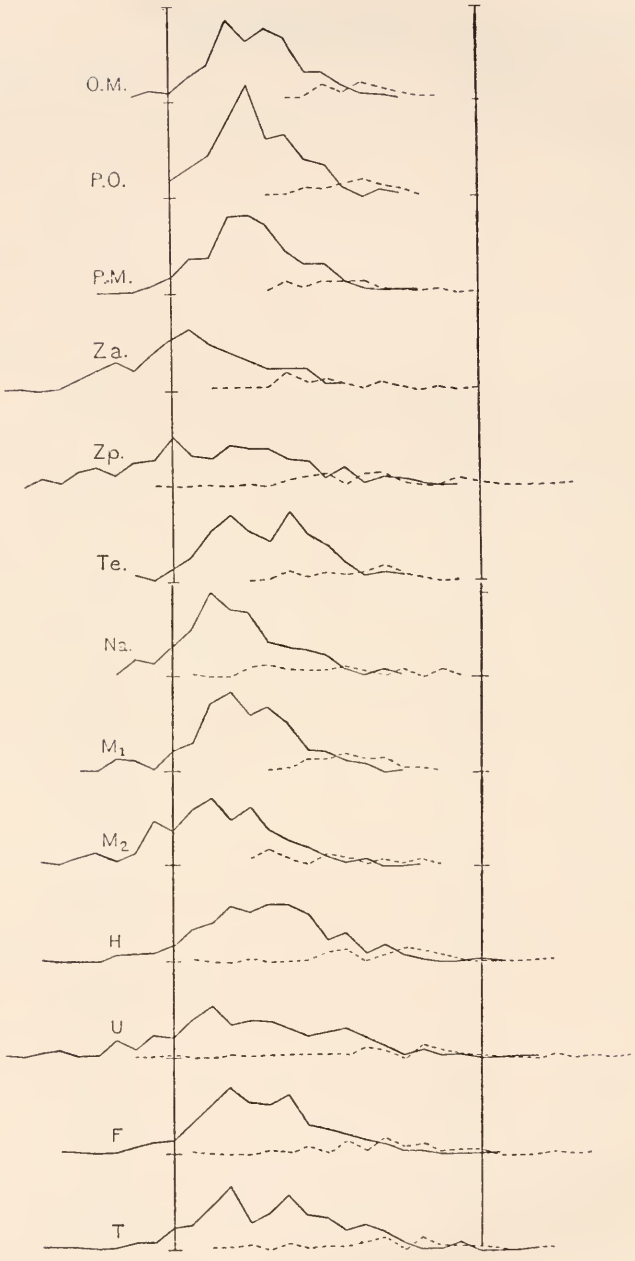


FIGURE 9.

Graphic representation of the summaries given in table 7 of the classes of F_1 and back-cross (with father) offspring as regards each measurement taken. The F_1 distribution is shown by the broken line; the back-cross distribution by the unbroken line.

STUDIES OF ADULT WEIGHT.

GROWTH CURVES.

The growth curves mentioned on page 25 were plotted on sheets of coordinate paper 20×24 inches from weights that were taken in most cases every week, giving an average of about 56 observations for each curve. Curves were made for nearly all of the animals. When this investigation was started it was supposed that weight would be the main character studied. It was believed that the growth curves would clearly show the adult weights, and that a comparison of the curves of a litter of F_1 animals with those of a litter of back-cross animals might picture their relative variability. A study of about 300 growth curves has shown that this is not the case. To obtain rabbit curves that would be smooth enough to determine the adult weights with accuracy would require more perfect experimental conditions than have been possible. But unfavorable conditions are by no means the only causes of trouble in dealing with these curves. In many cases the animals have begun to accumulate fat soon after maturity and at fifteen months their curves have shown no signs of flattening. In other cases the accumulation of fat has begun after a year, so that the fat curve and the growth curve proper are easily separable. Pregnancies and nursing occasion much uncertainty in estimating the adult weights of F_1 females. For a period of ten weeks pregnant females were weighed three times a week that the form of a normal pregnancy curve might be found, which would assist in disentangling the curves of breeding females. No uniformity could be found in these curves.

The most important information the growth curves afford is in vouching for the recovery of animals that have been sick; for, in spite of fluctuations, the trace of a regular curve can be seen in nearly every one. It soon becomes possible to determine whether at a certain point an animal is below or above its normal, through a recognition of the normal type of curve. Based on this element of regularity, which (when shown by a part of a litter) gives the type of curve the others would be expected to have followed, adult weights for the animals were estimated. Approximations were made within 100 grams, in a few cases within 50 grams.

COEFFICIENTS OF VARIABILITY.

Since absolute means can be found and the coefficients of variability calculated, weights have an advantage; but this can only slightly offset the uncertainty of their exactness. Coefficients of variability are given in table 8 for the adult weights of the various F_1 and back-cross fraternities. Most of the coefficients of the back-cross animals are higher than those for F_1, but some are as low as the coefficients of the F_1 fraternities. It should be stated that the two litters in the F_1 fraternity of family 1493 were found to have very different coefficients,

namely, 10.43 and 4.24. It is fair to compare their coefficient taken together (8.75) with other fraternities consisting of more than one litter.

TABLE 8.—*Coefficients of variability in weight of the several families of rabbits studied.*

Family No.	Coefficient variability in F_1.	Number of F_1 individuals.	Coefficient variability in back-cross with father.	Number of back-cross individuals.
647.....	5.16	4	10.52	5
			5.88	6
			10.27	7
1471.....	4.09	7	13.62*	7*
1491.....	6.22	4	10.46	10
			6.32	7
1493.....	8.75	15	13.56	8
			8.30	8
			9.29	12
			9.94	6
1531.....			13.46	16
			10.45	14
1532.....			10.27	10
1537.....			7.35	10
			8.23	13
2037.....			10.83	23

*In this case the back-cross was with the mother.

SUMMARY.

The weights, then, show a tendency for back-cross fraternities to be more variable than F_1 fraternities, although five back-cross fraternities in 16 showed no greater variability than some F_1 fraternities. Although not exact, the weights indicate the same fact that was shown by the bone measurements—namely, that there is a greater variability in the second than in the first generation of hybrids.

CONCLUSIONS.

EXPERIMENTAL.

The conclusion to be drawn from all these observations is clear. Whether on the basis of the comparison of the ranges of litters of the first filial generation with those of their corresponding back-crosses, or whether on the basis of the relative variability of the two generations, as shown by the standard deviations of the coefficients of size, or by the distribution of frequencies in relation to the parents or grandparents, or, finally, by their body weights, there is found a consistently greater diversity of sizes in the back-cross than in the first-hybrid generation. Characters occur among the second generation that are smaller than the corresponding characters in the small parent; others that are above the modes of the first generation large parents.

This difference in the two generations appears in spite of a fact that might be expected to hide it. Several of the original mothers were undoubtedly partially heterozygous in size, as is shown by their pedigrees (table 3). This would lead one to expect a greater variability in their offspring from crosses with the small male than was shown by

their own fraternities, if we assume that gametes bearing characters for different sizes do not indissolubly join their size-determining substances. If the variability of F_1 is really partly caused by a segregation, the difference between the variabilities of the two generations is due to the fact that the parents of the heterozygous mothers differed in fewer factors than did the parents of the F_1 generation. If the mixed nature of the females' pedigrees is claimed to influence the results, it can only make the difference in variability more significant.

This work and that of Philips (1912) on ducks show that in animals quantitative characters may give increased variability in the second generation, as has been previously shown to be true for plants. Many of the cases that have been presented have similarities. They all deal with heritable characters, quantitatively different. To a greater or less degree, they are subject to fluctuations that, not being heritable, may be roughly ascribed to environment. When crosses between extremes are made, hybrids are formed generally of an intermediate nature. In the following generation new forms appear that are similar to the original parents or even more extreme, although the majority of the individuals are intermediate. In certain cases crosses between similar varieties or lines, after an F_1 like the parents, give second generations in which a wide range of grades is found.

These are the facts and this is all that can be definitely ascertained from the work that has already been completed. Having been found to occur a few times, it is supposed that these phenomena will always be the same. Yet we know that it is only a probability. On this probability we build a law, a general statement or description of the facts, which stands until new facts demand a new statement. In this case such a law may be stated:

The second generation of a size cross shows greater diversity than does the first generation or the parental lines. Size characters that are inherited in a Mendelian fashion are included in the above statement.

All practical application must come from this fact.

THEORETICAL.

When the reason for this increased variability is asked or when its mechanism is suggested we reach the realm of hypothesis and supposition, yet very little interest is found in facts unrelated to explanatory theories. Mendel's papers passed through a long dormant period; his letters to Nägeli failed to excite interest. When their theoretical significance was once realized, they received wide attention.

The theory of multiple units has been developed in Part I. From cases of color inheritance in which very definite ratios suggest the presence of two or more independent units we came to cases of structural characters which give similar ratios to their absence (ligulæ, Rispentypen). So we have the same basis for assuming two or more

independent units for certain morphological characters as for certain color characters. From structural characters that can be absent and thus make ratios recognizable, to those in which the "recessive" forms can not be distinctly separated, is a short step. The phenomena shown by these two types of characters are strikingly similar. Both show wide variations in F_2 not found in the parental or first hybrid generations. Both types show similar wide variations after crosses between certain strains that appear to be alike. The appearance of *Fahnentypen* in crosses between *Rispentypen* is an example of the type which gives definite ratios; crosses between long beets that give very long forms is an example of the type which does not afford ratios. Any theory to account for the wide variations in F_2 of crosses involving characters of this latter type must also account for this similarity with cases where ratios are found and, again, with cases where simple Mendelian ratios and complex ones are found for the same character-differences.

The conception of many independent units presented by Nilsson-Ehle can be applied to all the facts. It is the logical outcome of the pure-line doctrine of de Vries and Johannsen; in its breadth of application and its comprehensibility this theory, based on the purity of gametes and unit factors, is very attractive. Through its use as a working hypothesis important facts have been discovered and an important system of inheritance has been developed.

Castle (1912) has shown that this hypothesis is not the only one that can be raised to satisfy the facts here presented. He says:

> "If size differences are due to quantitative variations in special materials within the cell, it is not necessary to suppose that these materials are localized in chunks of uniform and unvarying size, or that they occur in any particular number of chunks. Yet the genotype hypothesis involves one or both of these assumptions. Both are unnecessary. Variability would result whether the growth-inducing substances were localized or not, provided only they were not homogeneous in distribution throughout the cell. Crossing would increase variability beyond the first generation of offspring, because it would increase the heterogeneity of the zygote in special substances (though not in its total content of such substances) and this heterogeneity of structure would lead to greater quantitative variation in such materials among the gametes arising from the heterozygote. Thus greater variability would appear in the second hybrid generation. As a matter of fact we know that protoplasm is not homogeneous, and that there are substances widely distributed in the cell, not localized in chromosomes, which may well have an influence on size."

To this East (1912) replied, making a very clear presentation of the case of multiple factors. He claims qualitative characters can be described in the same way and that one does not gain a system thereby.

At present it seems that there is recorded more actual work favoring the hypothesis of multiple factors than any alternative hypothesis.

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APPENDIX.

THE NATURE OF SIZE FACTORS AS INDICATED BY A STUDY OF CORRELATION.

BY W. E. CASTLE.

To determine to what extent the several bone measurements studied by Dr. MacDowell vary independently of each other, I asked Messrs. S. Wright and H. D. Fish to form correlation tables between the more important measurements taken (see tables 9–19). Their work is based on the measurements of Dr. MacDowell, which he kindly put at their disposal. All possible correlations were studied between the five measurements, O. M., Zp., H., F., and T. These include one measurement of skull length, one of skull width, one of a bone of the front leg, and two of bones of the hind leg. The ten correlation coefficients calculated are all positive and fairly high. The lowest, 0.658, is between skull width and length of tibia; the highest, 0.858, is between femur and tibia, two successive bones of the hind leg, but the correlation between femur and humerus is practically the same, 0.857. Skull length (O. M.) is more nearly uniform in its correlation with the other measurements studied than any of the other four measurements. Its coefficient varies only from 0.70 to 0.76. The former coefficient is given by the femur correlation, the latter by the tibia; but as femur and tibia are themselves very closely correlated, more so than any other pair of measurements, it follows that neither correlation with the skull length can in the long run be very different from the other. Hence skull length is probably the best *single* measurement that could be taken as a basis for comparing the size of individual rabbits. It happens (not without reason, probably) that this particular measurement is one commonly employed in systematic descriptions of rodents. A more fortunate selection could apparently not have been made.

In view of the high correlations obtaining between one skeletal dimension and another (and these agree closely with those observed in the case of man by Pearson and others), it follows that to a large extent the factors which determine size are *general* factors affecting all parts of the skeleton simultaneously. When the skull is long, the legs are long and the skull is wide, and every other part varies in proportion (or within 65 to 85 per cent of the same proportion). Whatever special factors (if any) there are, which are concerned in limiting the size of particular bones, these can play only a subordinate part in determining size. The chief factors are plainly *general* factors and control

the growth of the body as a whole. What makes the difference between a big rabbit and a small one is clearly a quantitative difference in these general factors, or it is something which modifies the action of these general factors, which amounts to the same thing. That which determines the adult size of a rabbit determines (if other conditions remain constant) both the rate at which it grows and the time when growth ceases. A large race of rabbits has a steeper growth curve than a small race and the period of growth continues longer (see Castle *et al.*, 1909). The proportions of the body also change in a constant direction as growth proceeds. For example, the larger a rabbit becomes the more elongated its skull becomes. Is a larger size attained in one race simply because growth *continues* longer, or is the character of growth different from the beginning? A study of immature rabbits of large and small races at corresponding absolute size stages might throw light on this question.

TABLE 9.—*Correlation between the measurements O. M. and Zp. in the rabbits studied. r=0.750.*

O. M. / Zp.	6.6–	6.8–	7.0–	7.2–	7.4–	7.6–	7.8–	8.0–	8.2–	8.4–	8.6–	8.8–	9.0–	
3.6–	1													1
3.7–	6	3	5	2										16
3.8–	4	14	19	15	4									56
3.9–		6	27	32	13	1								79
4.0–		3	13	33	25	6	3	1						84
4.1–		1	2	15	26	13	5		2					64
4.2–			3	3	11	13	10	4	1					45
4.3–				1	4	4	5	5		1				20
4.4–						1			2		1		1	5
4.5–								3	1				1	5
	11	27	69	101	83	38	23	13	6	1	1		2	375

TABLE 10.—*Correlation between the measurements O. M. and H. r=0.743.*

O. M. / H.	6.6–	6.8–	7.0–	7.2–	7.4–	7.6–	7.8–	8.0–	8.2–	8.4–	8.6–	8.8–	9.0–	
6.0–		1	2											3
6.2–	5	8	11	6	3									33
6.4–	6	14	34	33	13	2								102
6.6–		5	21	46	32	15	2	1						122
6.8–			1	16	27	14	11	1	1					71
7.0–					7	4	8	7	1	1	1			29
7.2–						3	2	3	3					11
7.4–								1					1	2
7.6–														
7.8–													1	1
	11	28	69	101	82	38	23	13	5	1	1		2	374

TABLE 11.—*Correlation between the measurements O. M. and F.* $r = 0.760$.

O. M. / F.	6.6–	6.8–	7.0–	7.2–	7.4–	7.6–	7.8–	8.0–	8.2–	8.4–	8.6–	8.8–	9.0–	
7.6–	2	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	3
7.8–	5	8	5	5	4	.....	.....	.....	.....	.....	.....	.....	.....	27
8.0–	1	10	32	29	7	1	.....	.....	.....	.....	.....	.....	.....	80
8.2–	2	9	24	39	19	6	1	.....	.....	.....	.....	.....	.....	100
8.4–	.....	.....	4	23	31	19	3	2	.....	.....	.....	.....	.....	82
8.6–	.....	.....	1	4	20	6	14	1	1	.....	.....	.....	.....	47
8.8–	.....	.....	.....	1	.....	6	4	6	1	1	1	.....	.....	20
9.0–	.....	.....	.....	....	1	.....	....	2	3	.....	.....	.....	....	6
9.2–	.....	.....	.....	.....	.....	.....	1	2	1	.....	.....	.....	1	5
9.4–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
9.6–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	1
	10	27	67	101	82	38	23	13	6	1	1	.....	2	371

TABLE 12.—*Correlation between the measurements T. and O. M.* $r = 0.702$.

T. / O. M.	8.8–	9.0–	9.2–	9.4–	9.6–	9.8–	10.0–	10.2–	10.4–	10.6–	10.8–	11.0–	
6.6–	1	4	4	1	1	.....	.....	.....	.....	.....	.....	.....	11
6.8–	.....	5	12	9	.....	.....	.....	.....	.....	.....	.....	.....	26
7.0–	.....	3	20	23	19	2	3	.....	.....	.....	.....	.....	70
7.2–	1	1	14	33	29	14	9	.....	.....	.....	.....	.....	101
7.4–	.....	1	8	15	18	20	17	3	1	.....	.....	.....	83
7.6–	.....	.....	.....	7	5	9	15	1	.....	.....	.....	.....	37
7.8–	.....	.....	.....	1	1	4	14	3	.....	.....	.....	.....	23
8.0–	.....	.....	.....	.....	1	2	6	1	3	.....	.....	.....	13
8.2–	.....	.....	.....	.....	.....	.....	2	1	3	.....	.....	.....	6
8.4–	.....	.....	.....	.....	.....	.....	1	.....	.....	.....	.....	.....	1
8.6–	.....	.....	.....	.....	.....	.....	.....	1	.....	.....	.....	.....	1
8.8–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
9.0–	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	.....	1	2
	2	14	58	89	74	51	67	10	8	.....	.....	1	374

TABLE 13.—*Correlation between the measurements H. and Zp.* $r = 0.675$.

H. / Zp.	6.0–	6.2–	6.4–	6.6–	6.8–	7.0–	7.2–	7.4–	7.6–	7.8–	
3.6–	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	1
3.7–	.....	5	10	1	.....	.....	.....	.....	.....	.....	16
3.8–	3	12	26	13	2	.....	.....	.....	.....	.....	56
3.9–	.....	9	32	30	8	1	.....	.....	.....	.....	80
4.0–	.....	5	20	36	21	2	.....	.....	.....	.....	84
4.1–	.....	.....	11	25	22	4	2	.....	.....	.....	64
4.2–	.....	1	2	15	14	11	3	.....	.....	.....	46
4.3–	.....	.....	.....	4	4	8	4	.....	.....	.....	20
4.4–	.....	.....	.....	.....	.....	2	1	1	.....	.....	4
4.5–	.....	.....	.....	.....	.....	2	1	1	.....	1	5
	3	32	102	124	71	30	11	2	.....	1	376

TABLE 14.—*Correlation between the measurements F. and Zp. r = 0.674.*

F. / Zp.	7.6–	7.8–	8.0–	8.2–	8.4–	8.6–	8.8–	9.0–	9.2–	9.4–	9.6–	
3.6–	.....	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	1
3.7–	1	5	7	1	1	.....	.....	.....	.....	.....	.....	15
3.8–	2	10	21	15	5	1	1	.....	.....	.....	.....	55
3.9–	.....	7	26	30	10	5	1	.....	.....	.....	.....	79
4.0–	.....	3	20	32	21	9	1	1	.....	.....	.....	87
4.1–	.....	2	6	12	28	12	2	1	.....	.....	.....	63
4.2–	.....	.....	.....	8	13	13	9	1	.....	.....	.....	44
4.3–	.....	.....	.....	2	4	7	5	0	2	.....	.....	20
4.4–	.....	.....	.....	.....	.....	.....	3	1	1	.....	.....	5
4.5–	.....	.....	.....	.....	.....	.....	.....	2	2	.....	1	5
	3	27	80	101	82	47	22	6	5	.....	1	374

TABLE 15.—*Correlation between the measurements T. and Zp. r = 0.658.*

T. / Zp.	8.8–	9.0–	9.2–	9.4–	9.6–	9.8–	10.0–	10.2–	10.4–	10.6–	10.8–	11.0–	
3.6–	.....	.....	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	1
3.7–	1	4	6	4	1	.....	.....	.....	.....	.....	.....	.....	16
3.8–	.....	7	20	16	8	4	1	.....	.....	.....	.....	.....	56
3.9–	1	2	18	22	23	7	7	.....	.....	.....	.....	.....	80
4.0–		1	11	29	17	12	11	2	1	.....	.....	.....	84
4.1–	.....	.....	3	14	16	14	13	2	1	.....	.....	.....	63
4.2–	.....	.....	.....	3	8	13	18	3	1	.....	.....	.....	46
4.3–	.....	.....	.....	.....	2	1	15	1	1	.....	.....	.....	20
4.4–	.....	.....	.....	.....	.....	.....	2	2	1	.....	.....	.....	5
4.5–	.....	.....	.....	.....	.....	.....	1	.....	3	.....	.....	1	5
	2	14	58	89	75	51	63	10	8	.....	.....	1	376

TABLE 16.—*Correlation between the measurements F. and H. r = 0.857.*

F. / H.	7.6–	7.8–	8.0–	8.2–	8.4–	8.6–	8.8–	9.0–	9.2–	9.4–	
6.0–	1	2	1	.....	.....	.....	.....	.....	.....	.....	4
6.2–	2	16	13	4	.....	.....	.....	.....	.....	.....	35
6.4–	.....	9	51	32	4	.....	.....	.....	.....	.....	96
6.6–	.....	.....	13	52	47	4	.....	.....	.....	.....	116
6.8–	.....	.....	1	10	29	29	4	.....	.....	.....	73
7.0–	.....	.....	.....	.....	3	13	13	4	.....	.....	33
7.2–	.....	.....	.....	1	.....	1	4	1	3	.....	10
7.4–	.....	.....	.....	.....	.....	.....	.....	.....	2	.....	2
7.6–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
7.8–	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	1
	3	27	79	99	83	47	21	5	5	1	370

TABLE 17.—*Correlation between the measurements T. and H. r=0.791.*

T. / H.	8.8–	9.0–	9.2–	9.4–	9.6–	9.8–	10.0–	10.2–	10.4–	10.6–	10.8–	10.10–	
6.0–	.....	1	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	3
6.2–	2	8	16	4	3	.....	.....	.....	.....	.....	.....	.....	33
6.4–	.....	4	32	45	16	2	2	.....	.....	.....	.....	.....	101
6.6–	.....	1	6	37	43	19	17	.....	.....	.....	.....	.....	123
6.8–	.....	.....	2	3	12	22	27	4	.....	.....	.....	.....	70
7.0–	.....	.....	.....	.....	.....	8	17	2	3	.....	.....	.....	30
7.2–	.....	.....	.....	.....	.....	.....	5	3	3	.....	.....	.....	11
7.4–	.....	.....	.....	.....	.....	.....	.....	.....	2	.....	.....	.....	2
7.6–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
7.8–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	1
	2	14	58	89	74	51	68	9	8	.....	.....	1	374

TABLE 18.—*Correlation between the measurements F. and T. r=0.858.*

F. / T.	7.6–	7.8–	8.0–	8.2–	8.4–	8.6–	8.8–	9.0–	9.2–	9.4–	9.6–	
8.8–	.....	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	2
9.0–	3	7	3	1	.....	.....	.....	.....	.....	.....	.....	14
9.2–	.....	17	31	7	2	.....	.....	.....	.....	.....	.....	57
9.4–	.....	.....	34	45	7	1	.....	.....	.....	.....	.....	87
9.6–	.....	1	12	37	21	3	.....	.....	.....	.....	.....	74
9.8–	.....	.....	.....	7	31	10	2	.....	.....	.....	.....	50
10.0–	.....	.....	1	2	20	30	13	1	1	.....	.....	68
10.2–	.....	.....	.....	.....	.....	3	6	1	.....	.....	.....	10
10.4–	.....	.....	.....	.....	.....	.....	.....	4	4	.....	.....	8
10.6–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
10.8–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
11.0–	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	1
	3	27	81	99	81	47	21	6	5	.....	1	371

TABLE 19.—*Summary of the statistical constants obtained from Tables 9–18.*

Measurement.	Mean.	σ	C. V.	Correlated with.	r
O. M.	7.30	0.36	49.3	Zp.	0.750
				H.	0.743
				F.	0.760
				T.	0.701
Zp.	4.00	0.17	42.5	H.	0.675
				F.	0.674
				T.	0.658
H.	6.60	0.26	39.4	F.	0.857
				T.	0.791
F.	8.28	0.31	37.4	T.	0.858
T.	9 60	0.34	35 4	.....	.....

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